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Influence of the El Niño Southern Oscillation and wetland condition on the abundance and spatial distribution of two flamingo species in lowland wetlands of central Argentina

Research Article

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Summary

Birds show considerable spatial and temporal fluctuations in their abundance due to variations in habitat conditions. The lowland wetlands of the Pampas region in Argentina are key wintering areas for two flamingo species. The Chilean Flamingo *Phoenicopterus chilensis* is a year-round resident, while the Andean Flamingo *Phoenicoparrus andinus* is a partial altitudinal migrant that uses these wetlands in winter when some of the wetlands in the high Andes freeze over. We studied the association between the annual abundance of both flamingo species, wetland condition (water surface area and water salinity), and environmental conditions (flooding) driven by the El Niño Southern Oscillation (ENSO) over 15 consecutive winters (July–August 2008–2022) in 24 lowland wetlands in central Argentina. There were notable differences in wetland surface area and water conductivity between years, with some wetlands ranging from flooded to almost dried out. For any given year, there were also large differences in water surface area and water conductivity between wetlands. Both flamingo species showed marked fluctuations in abundance over the study period. Each year, the Chilean Flamingo was more abundant than the Andean Flamingo. The Chilean Flamingo was recorded at least once in every wetland, while the Andean Flamingo was absent from three wetlands and was not observed in two years during the study. The Chilean Flamingo was recorded in wetlands covering a larger range of water conductivity values than the Andean Flamingo (2.53–58.23 ms/cm vs 2.94–16.20 ms/cm, respectively). The abundance of both flamingo species was higher at intermediate water conductivity values and decreased at higher or lower values. These results show that these lowland wetlands are subjected to strong interannual variation in climatic conditions which affect lake conditions, and thus the abundance of both flamingo species, highlighting the importance of conserving wetlands encompassing a broad range of environmental conditions.

Introduction

Large interannual cyclic variations in climatic conditions are associated with the El Niño Southern Oscillation (ENSO), a global phenomenon that has an extensive influence worldwide (Jaksic 2004). During an El Niño episode, strong rainfall occurs in some regions while severe droughts arise in other areas. The opposite pattern is observed during the La Niña episodes (Timmermann et al. 2018). These interannual variations in climatic conditions affect large wetland areas, which range from flooding conditions during wet cycles to drought conditions in dry ones (Guerra et al. 2019). The populations of many waterbird species living in these wetlands are affected by these marked variations in their habitats, which affect the availability of suitable sites for feeding, resting or breeding (Nores 2024; Romano et al. 2005; Senner et al. 2018). For instance, the abundance and distribution of waders and flamingos, which obtain their food from mud shores and salt pans of shallow saline environments (Mascitti 2001; Mascitti and Kravetz 2002), are deeply affected by interannual variations in climatic conditions that produce large variations in the availability of these habitats (Álvarez et al. 2018; Bucher and Curto 2012; Cézilly et al. 1995; Githaiga 2022; Nores 2024; Senner et al. 2018; Vargas et al. 2008).

Three of the six flamingo species in the world are found in southern South America (https://birdsoftheworld.org/bow/species/phoeni1/cur/introduction). The Chilean Flamingo *Phoenicopterus chilensis* has a widespread distribution, living in a variety of habitats from shallow saline wetlands in the high Andes to coastal wetlands throughout the Southern Cone (Bucher 1992; Sosa and Martín 2012). The Andean Flamingo *Phoenicoparrus andinus* and the Puna (or James's) Flamingo *Phoenicoparrus jamesi* are partial altitudinal migratory species that seasonally move from breeding areas in the high Andes to wintering areas in the lowland wetlands in Argentina and the coasts of Peru, and occasionally in coastal Brazil (Caziani et al. 2007; Derlindati et al. 2024; Ortiz et al. 2023). The Andean and Puna flamingos feed mainly on smaller microorganisms, such as diatoms, whereas the Chilean Flamingo feeds on a broader spectrum of phytoplankton and zooplankton (Ortiz et al. 2020; Polla et al. 2018; Tobar et al. 2012, 2014). Food availability in these saline environments depends on the presence of shallow waters and mudflats, as well as on water salinity (Battauz et al. 2013; Frau et al. 2015). Annual variation in the water level of the wetlands may affect habitat availability and salinity and hence food availability (phytoplankton and zooplankton) (Bucher and Curto 2012; Romano et al. 2017).

In the high Andes, all three flamingo species are nomadic at the local scale, moving among wetlands in search of suitable areas for breeding, feeding or resting (Caziani et al. 2007). In lowland wintering areas in Argentina, Andean and Chilean flamingos live in sympatry (Brandolin and Blendinger 2016; Bucher 1992; Caziani et al. 2007; Romano et al. 2008, 2017). The southernmost wintering area for Andean flamingos is Pampa de las Lagunas, a large system of wetlands with numerous saline water-bodies that differ in their geological origin, size, and depth, as well as in water chemistry (Iriondo and Kröhling 2007; Racca and Canoba 2014; Ragonese and Covas 1947). This high spatial heterogeneity represents a wide variation in habitat and food availability for flamingos. In addition, these wetlands also show high interannual variability in water level due to the ENSO rainfall cycling (Aragón et al. 2010; Guerra et al. 2019). During the dry years of the cycle, the water surface area of these shallow saline lakes decreases, leading to an increase in water salinity, and some of them completely dry out (Guerra et al. 2015). In contrast, during the wet years of the cycle, the increase in water surface area floods the area surrounding the saline lakes, reducing water salinity, and leaving very few shallow mudflats (Guerra et al. 2015).

The spatial and temporal distribution and abundance of flamingos and their relationships to variations in water surface area and water salinity of wetlands have scarcely been studied at a regional scale (Githaiga 2022), thus the goal of this study was to elucidate these relationships in two flamingo species using a diversity of wetlands. We used a long-term data set based on 15 flamingo surveys (2008–2022) carried out in winter (July–August) in 24 saline lakes in the Pampa de las Lagunas wetland system, Argentina, where Andean and Chilean flamingos co-occur, to analyse the effects of surveyed wetland characteristics (i.e. water surface area and water salinity) and environmental characteristics (i.e. flooding condition) in the survey year on the abundance and distribution of these two flamingo species.

Regarding spatial distribution within a year, we expected to find (1) higher flamingo abundances in wetlands with intermediate to high water salinity, and lower flamingo abundances in wetlands with low or very high water salinity due to higher food availability at intermediate salinity ranges, and (2) an increase in flamingo abundance with wetland size due to increased suitable habitat availability (Figure 1). Regarding temporal variation, we expected to find (3) a decrease in flamingo abundance in El Niño years (i.e. higher annual flooding conditions) due to a decrease in suitable habitat availability (i.e. mud shores) and water salinity, but also a decrease in flamingo abundance in strong La Niña years when some wetlands dry out (Figure 1). In addition, the effects of the El Niño will depend on wetland characteristics. In strong La Niña years, low rainfalls and high evaporation led to increasing water salinity and drying out of some small wetlands. Thus, we expected (4) flamingo relative abundance in La Niña years to be higher in wetlands with lower water salinity, but (5) lower in smaller wetlands (Figure 1). Finally, based on differences in diet breadth and habitat use between flamingo species, we expected Andean Flamingos to be present in (6) a narrower salinity range of wetlands (spatial distribution), and (7) a narrower range of flooding conditions (temporal distribution).

Methods

Conservation status of the study species

The Chilean Flamingo is classified as "Near Threatened" by the International Union for Conservation of Nature (IUCN) (BirdLife International 2018), listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and in Appendix II of the Convention on Migratory Species (CMS). For Argentina, it is considered "Vulnerable" (Ministerio de Ambiente y Desarrollo Sustentable and Aves Argentinas 2017). The Andean Flamingo is classified as "Vulnerable" by IUCN (BirdLife International 2020), listed in Appendix II of CITES and Appendix I of CMS, and has been included in the US Endangered Species Act. In Argentina, it is considered "Endangered" (Ministerio de Ambiente y Desarrollo Sustentable and Aves Argentinas 2017).

Study area

The Pampa de las Lagunas wetland system in Santa Fe Province, Argentina is in one of the largest agricultural areas in the world. It has a relatively flat topography, dotted with numerous saline wetlands, which are patches of high biodiversity embedded in a highly

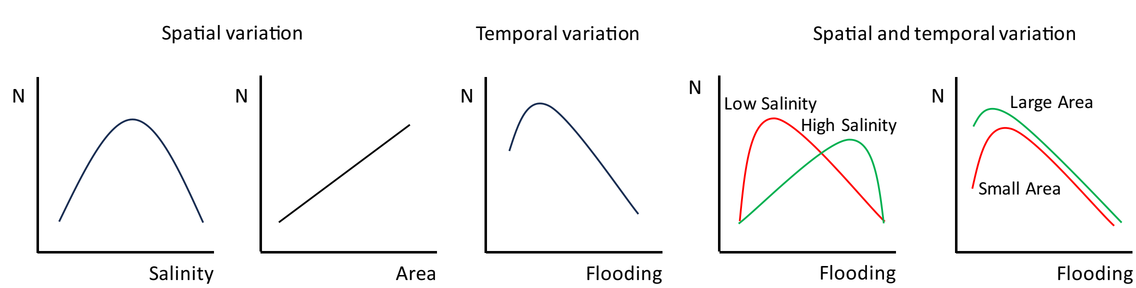

Figure 1. Predictions of the spatial, temporal, and spatial and temporal variation in flamingo abundance (N) among wetlands with differences in water salinity (Salinity) or water surface area (Area) and years with different flooding conditions (Flooding). For the simultaneous spatial and temporal variation two curves with contrasting salinity or area are shown.

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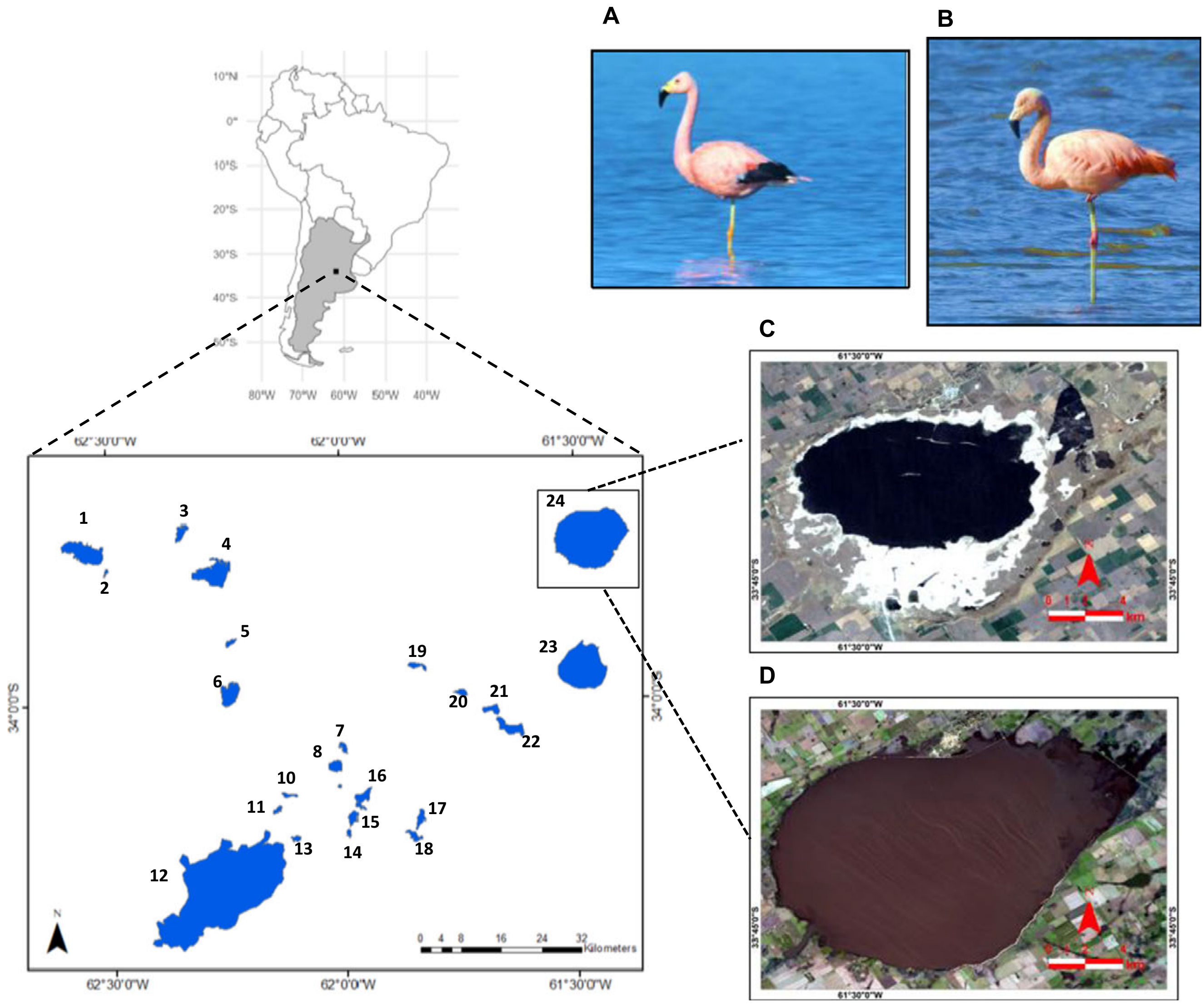

Figure 2. Location of the Pampa de las Lagunas study area within the Pampa region of central Argentina. The blue polygons in the lower left square denote the study wetlands: 1 = Las Tunas, 2 = La Dulce, 3 = La Badenia, 4 = Maggiolo, 5 = M1, 6 = Sancti Spiritu, 7 = MT2, 8 = MT3, 9 = MT4, 10 = Carmen Norte, 11 = Carmen Sur, 12 = La Picasa, 13 = Picasa 2, 14 = Los Flamencos, 15 = Bella Vista, 16 = Martín García, 17 = Morgan Norte, 18 = Morgan Sur, 19 = Encadenada 1, 20 = Encadenada 3, 21 = Encadenada 4, 22 = Encadenada 5, 23 = Quirno, 24 = Melincué. (A) Andean Flamingo *Phoenicoparrus andinus*; (B) Chilean Flamingo *Phoenicopterus chilensis*; (C) and (D) satellite images of Laguna Melincué during dry and wet years, respectively. (Photographs: (A) M. Romano; (B) J. Asmus)

simplified agricultural matrix (Figure 2). These saline wetlands differ in their geological origin (i.e. aeolian, tectonic blocks, etc.), size and depth (Iriondo and Kröhling 2007; Racca and Canoba 2014), and water chemistry (Ragonese and Covas 1947). The climate is temperate and humid, characterised by the penetration of moist air masses from the South Atlantic Ocean (Aliaga et al. 2017).

Flamingo count surveys

We carried out total count surveys of Andean and Chilean flamingos for 15 consecutive years during winter (July–August 2008–2022) in 24 wetlands in the Pampa de las Lagunas wetland system (see Supplementary material Tables S1 and S2). Not all wetlands could be surveyed in some years due to logistical problems (Table S2). We followed the methods used in the International Simultaneous Surveys of High Andean Flamingos carried out every five years by the Grupo de Conservación Flamencos Altoandinos (Caziani et al. 2007; Marconi 2010; Marconi et al. 2020). We counted flamingos from the shore with spotting scopes (15/45 × 60). At each wetland, we surveyed the entire area using point counts, adjusting the number of point counts to the size of the wetland and accessibility (Bibby et al. 2000). For each wetland, we increased the number of survey locations in high-water surface years. Flamingo counts were performed by the same observers (MR and IMB) every year. When the number of individuals in a group was several hundred and the density was homogeneous, we counted the number of blocks estimated to contain 10 or 100 individuals (Bibby et al. 2000).

Wetland characteristics (water conductivity measurements, water surface area) and environmental characteristics (flooding condition) driven by ENSO

We used water conductivity as a proxy for water salinity. For each wetland, after carrying out the flamingo survey, we determined the water conductivity (mS/cm) *in situ* using a multiparametric probe

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(Lutron YK-2001 and Lutron WA-2015, Lutron, Coopersburg, PA, USA). We estimated water salinity (g/L) from water conductivity following Dejoux (1993). We classified wetlands according to their water salinity following Hammer (1986): subhaline (0.5–3 g/L), hypohaline (3–20 g/L), mesohaline (20–50 g/L), and hyperhaline (>50 g/L).

We downloaded cloudless satellite images (Landsat 5 TM 1984–2011; Landsat 7 ETM 1999–2014; Landsat 8 OLI_TIRS 2013–2015, US Geological Survey; NASA) corresponding to the flamingo counting date or nearby days to calculate the water surface area (km^2) of each wetland using ArcGis 10.5.

The El Niño 3.4 index is considered representative of the ENSO phenomenon (Barnston et al. 1997), thus for each annual survey, we downloaded monthly ENSO index values from https://psl.noaa.gov/data/correlation/nina34.anom.data. The El Niño 3.4 index reflects anomalies in sea surface temperature, within a specific equatorial region of the Pacific Ocean. Values below -0.5°C indicate the development of the La Niña event, while anomalies of -1.5°C or lower denote a particularly intense La Niña event. Conversely, values exceeding 0.5°C indicate the presence of the El Niño event, and anomalies greater than 1.5°C indicate a very strong El Niño event.

Derived variables

To characterise the size and salinity of each wetland, we calculated the mean water surface area (Mean Area) and the mean water conductivity (Mean Conductivity) for each wetland throughout the study period (Figure S1). To characterise the annual flooding conditions, for each wetland, we transformed the water surface area values into Z-scores, i.e. (observed value – mean of the sample)/ standard deviation of the sample), and then for each year we calculated the Mean Annual Z-score for the area of the study wetlands (Figure S1). This variable was used as a proxy for the annual flooding conditions due to climatic conditions ranging from very dry to very wet years (Aragón et al. 2010). A similar approach was used to calculate the Mean Annual Z-score for the conductivity of the study wetlands (Figure S1).

For each year in the study, we calculated the percentage of surveyed wetlands where the individuals of each flamingo species were recorded, and the relative dominance of individual distribution among wetlands by dividing the maximum number of individuals in a wetland by the sum of individuals for all wetlands.

Data analysis

We used general linear models to analyse the effects of the El Niño 3.4 Index on the Annual Z-scores for Area, as a proxy for the annual flooding conditions, and the impact of the latter on the Annual Z-scores for Conductivity. Then, we used general linear models to analyse the effects of the Annual Z-scores for Area on (1) the annual abundance and percentage of the surveyed wetlands used by each flamingo species, and (2) the annual relative dominance in the wetlands used by both flamingo species. The models were carried out with library glmmTMB (Brooks et al. 2017).

Based on the proposed hypotheses (Figure 1), we ran a general linear mixed model (glmm) for each flamingo species to assess the effect of the Annual Z-scores for Area and the mean conditions of each wetland (i.e. Mean Area and Mean Conductivity) on flamingo abundance. Mean Area and Mean Conductivity were ln-transformed and centred. The linear models were based on a zero-inflated negative binomial distribution, using Wetland and Year as random factors. Linear and polynomial models were compared using Akaike information criterion (AIC) selection (Zuur et al. 2009). We standardised the explanatory variables to reduce the correlations between the estimated coefficients for the linear and quadratic effects and to make the main effects biologically interpretable (Schielzeth 2010). The models were carried out with library glmmTMB, using nbinom2 to account for the linear and quadratic effects of the zero-inflated part (Brooks et al. 2017).

All analyses were performed in R (R Core Team 2023) and adjustments of model residuals were assessed using the DHARMa library (Hartig 2022).

Results

Spatial and temporal variation in water surface area and water conductivity

The surveyed wetlands differed in their Mean Area and Mean Conductivity (Table S1). There was a two-order of magnitude gradient in Mean Area (0.81–93.51 km^2) between the larger wetlands (e.g. La Picasa and Laguna Melincué) to the smaller ones (e.g. La Dulce, Los Flamencos, and MT4). There was also a notable gradient in Mean Conductivity (2.53–58.23 mS/cm) from some wetlands with very high salinity (e.g. Las Tunas and La Badenia; mesohaline wetlands; 20–50 g/L), to others with low salinity (e.g. Encadenada 1, Encadenada 4, and MT4; subhaline wetlands; (0.5–3 g/l) (Table S1). The Mean Area was not correlated with the Mean Conductivity among the surveyed wetlands ($r = 0.03$, $P = 0.89$).

The annual water surface area (Z-score Area) and the annual water conductivity (Z-score Conductivity) varied markedly throughout the study period (Figure 3). During the first five years (2008–2012), most wetlands showed smaller annual water surface areas and higher annual water conductivity than in later years (2015–2018) (Figure 3). In 2009 and 2011, eight wetlands almost dried out completely (Table S1), while in 2016 and 2017 some wetlands increased up to three times their average water surface area and then reduced their area again in later years (2018–2022) (Figure 3). The opposite pattern was recorded for annual water conductivity where it was high in the first four years of the study and decreased in the latter years (Figure 3). A rise in the El Niño 3.4 index increased flooding condition leading to higher annual water surface area (i.e. Mean Z-score for Area), which in turn decreased the annual water conductivity (i.e. Mean Z-score for Conductivity; Figure 3).

Annual variation in flamingo abundance and number of wetlands used

The abundance of each flamingo species, the number of wetlands where they were recorded, and the relative dominance between wetlands varied markedly among years (Figure 4). In each year of the study, the Chilean Flamingo was more abundant and recorded in more wetlands than the Andean Flamingo (Figure 4). The Chilean Flamingo was recorded in all years, whereas the Andean Flamingo had extremely low numbers in some years and was not recorded in 2016 and 2017. The annual abundance of both flamingo species and the annual number of wetlands used by the Andean Flamingo decreased when flooding (i.e. Annual Z-score for Area) was higher, while the number of wetlands used by the Chilean Flamingo was not affected by flooding. For both flamingo species, the relative dominance of individual distribution among wetlands was not affected by flooding (Figure 4).

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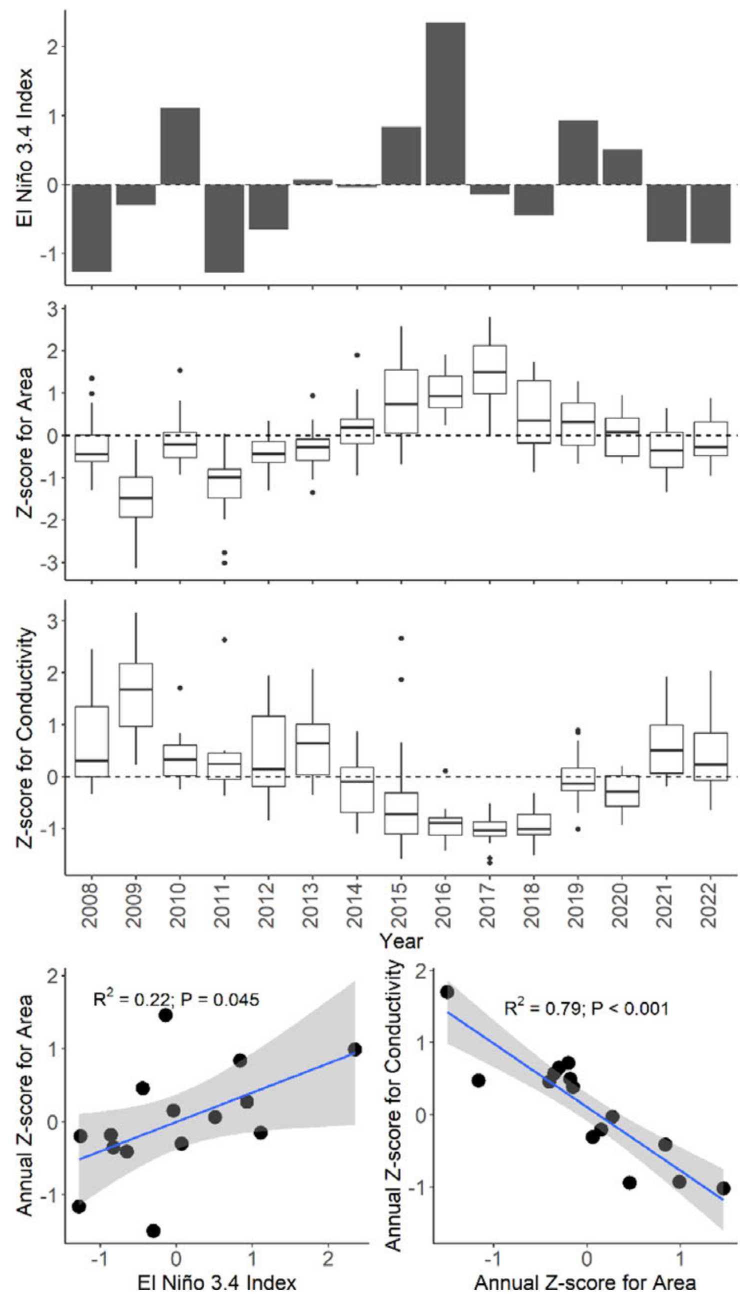

Figure 3. Annual variation of El Niño 3.4 index, the Z-scores of water surface area and water conductivity of the sampled wetlands throughout the study period (2008–2022), and relationships between the considered variables. The coefficients of determination (R^2) and probability values (*P*) are shown.

Spatial variation in flamingo abundance and the number of years when they were recorded

The abundance of each flamingo species and the number of years when they were recorded varied markedly among wetlands (Figure 5). The Chilean Flamingo was recorded in all wetlands, whereas the Andean Flamingo had extremely low numbers in some wetlands and was not recorded in three of them (Figure 5). For each wetland, except Melincué, the Chilean Flamingo was more abundant and recorded in more years than the Andean Flamingo (Figure 5). The abundance of individuals and the number of wetlands used by both flamingo species tended to increase with Mean Area but were not affected by Mean Conductivity (Figure 5). For both flamingo species, the relative dominance of individual distribution among wetlands was not affected by Mean Area or Mean Conductivity (Figure 5).

Species-specific responses of flamingos to annual flooding and wetland characteristics

Andean and Chilean flamingos differed in their response to annual flooding conditions (i.e. Annual Z-score for Area) and wetland characteristics (i.e. Mean Area and Mean Conductivity). The abundance of the Chilean Flamingo decreases with higher annual flooding conditions, and at similar flooding conditions, its abundance was higher in wetlands with higher mean water conductivity and mean area (Figures 6, S2, and S3). In contrast, the abundance of the

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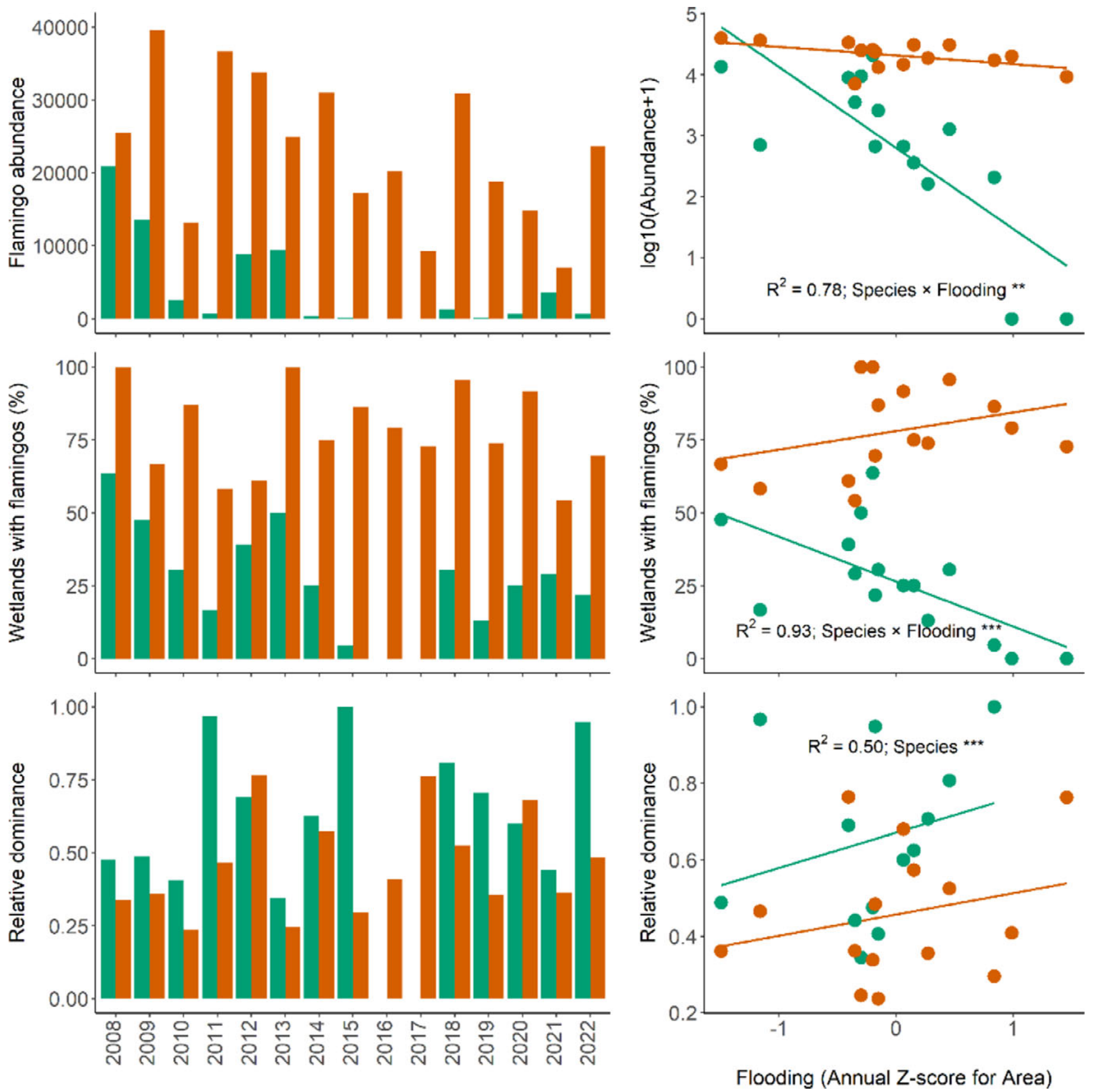

Figure 4. Individual abundance, percentage of surveyed wetlands, and relative dominance where Andean Flamingos (●) and Chilean Flamingos (●) were recorded each winter from 2008 to 2022 in Pampa de las Lagunas and Santa Fe Argentina, and their relationship with the flooding conditions (i.e. Annual Z-score for Area). Coefficients of determination (R^2) are shown. Statistically significant differences: ** = P <0.01, *** = P <0.001.

Andean Flamingo showed a quadratic response to the annual flooding conditions and the mean water conductivity of the wetland, and no effect on the mean water surface area of the wetland (Figures 6 and S2). For both flamingo species, there was an interaction between the annual flooding conditions and the mean water conductivity of the wetland. In years when wetlands were flooded, the flamingo abundances were higher in wetlands with higher mean water conductivity, whereas when flooding conditions were lower, flamingo abundances were higher in wetlands with medium water conductivity (Figures 6 and S2).

Discussion

Interannual variation in flamingo abundance at Pampa de las Lagunas

During the study period (2008–2022), there were marked differences among years in the abundance of Andean and Chilean flamingos in the Pampa de las Lagunas wetlands complex, but in all the sampled years, Chilean Flamingo abundances were always higher and less variable than the Andean Flamingo. These patterns may be due to differences in their movements (Caziani et al. 2007).

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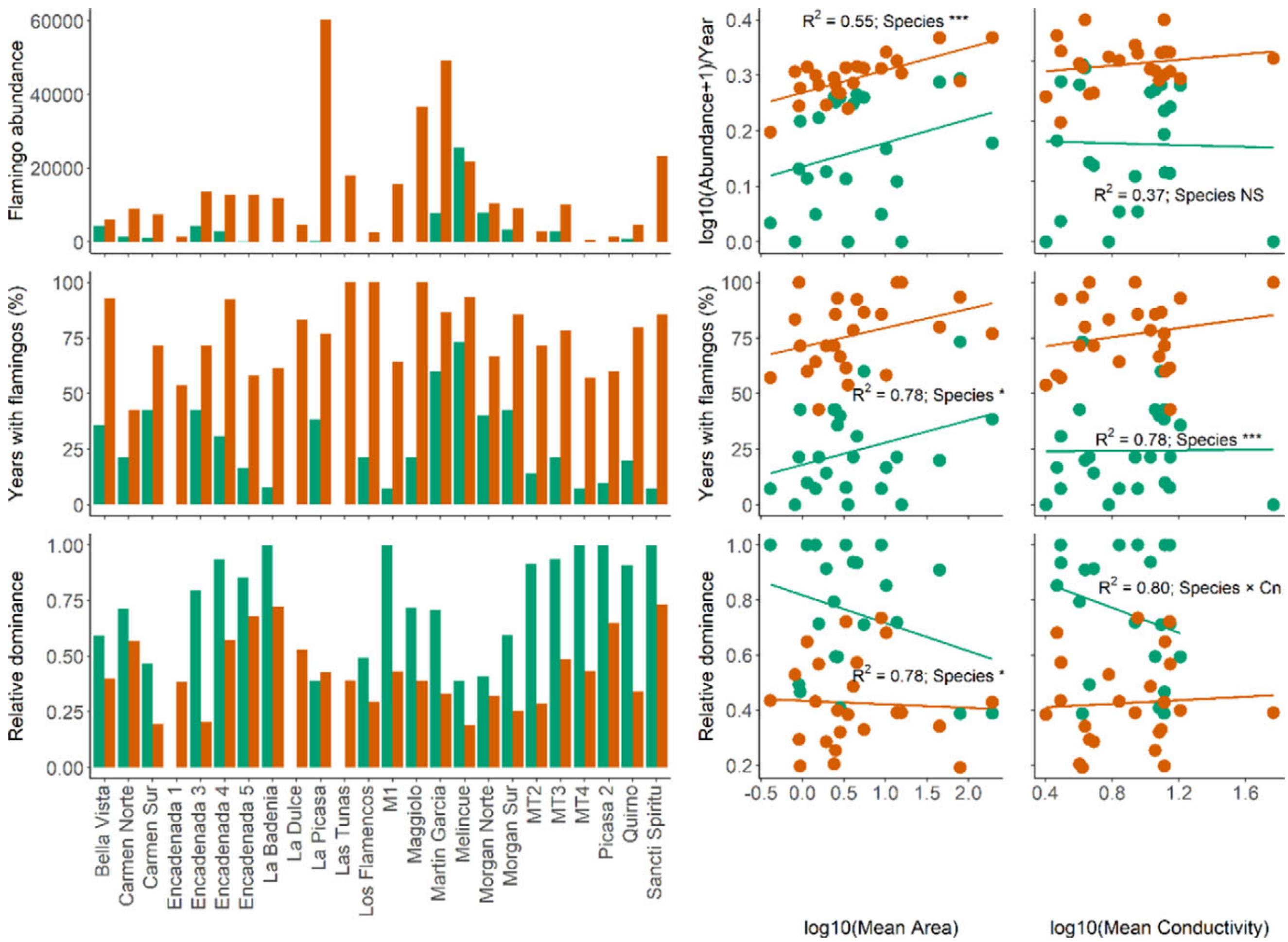

Figure 5. Individual abundance, percentage of years, and relative dominance when Andean flamingos (●) and Chilean flamingos (●) were recorded for each of the 24 wetlands in Pampa de las Lagunas and their relationship with the Mean Area and Mean Conductivity. Coefficients of determination (R^2) are shown. Statistically significant differences: * = P <0.05, *** = P <0.001, ns = >0.05.

The Chilean Flamingo is a resident species that most summers disperses to other lowland wetlands (e.g. Laguna Mar Chiquita) for breeding but returns to the Pampas de las Lagunas area in winter (Romano et al. 2005). In contrast, the Andean Flamingo is an altitudinal migratory species (Caziani et al. 2007) that uses wetlands in the study site as a wintering area (Romano et al. 2017).

Annual variations in the abundance of Andean and Chilean flamingos were associated with fluctuations in water surface area and water salinity due to the ENSO macro-climatic oscillations. During a satellite telemetry study that lasted five years (2003–2007), 5 of the 16 Andean flamingos with transmitters were recorded at our study sites, though none were recorded in all years, and none were recorded in 2003 (Romano et al. 2017), a very wet year when most lowland wetlands were flooded (Guerra et al. 2019). Similar patterns have been reported for these flamingo species at other sites in South America (Álvarez et al. 2018; Bucher and Curto 2012; Bucher et al. 2000; Mascitti 2001; Nores 2024), as well as for other flamingo species (Cézilly et al. 1995; Mawhinney 2008).

The abundance of Andean Flamingos at our study sites varied from about 20,000 individuals in the winter of 2008 (i.e. about 25% of the estimated world population; Marconi et al. 2020) to zero in the winter of 2015 and 2016, when the water table and the water surface area were high (Romano et al. 2017), suggesting that its presence is likely dependent on macroclimatic conditions imposed by the ENSO phenomenon. This phenomenon is characterised by warmer temperatures during the El Niño phase and cooler temperatures during the La Niña phase. However, the ENSO rainfall cycling produced opposite rainfall patterns in the high Andes of the Altiplano and Puna, the flamingos' summer range, compared with the lowlands of central Argentina (Garreaud and Aceituno 2001). In the Altiplano, during the warm phase of ENSO (El Niño), the rainfall pattern is characterised by lower rainfall and higher evapotranspiration (Lobos-Roco et al. 2022; Valdivielso et al. 2024). Consequently, in the Altiplano during the El Niño phase, water surface area decreased, and water salinity increased leading to a lower abundance of algae (Colla et al. 2022). The higher temperatures during the El Niño phase could increase physiological stress in flamingo species, posing a challenge as the migration season approaches, particularly complicating long-distance migration (O'Hara et al. 2007), mainly for individuals from more vulnerable age groups such as first-year or juvenile birds. In the case of the Andean Flamingo, in some winters some individuals could stop at an intermediate altitude in the Altiplano (e.g. Laguna de Los Pozuelos, Jujuy) or descend to lowland areas (e.g. Laguna Mar Chiquita, Córdoba), without reaching areas in its extreme southern distribution such as the Pampa de las Lagunas wetlands (Jahn et al. 2023). Landing (stop-over) instead of continuing the flight may be beneficial for accumulating energy and recovering physiologically

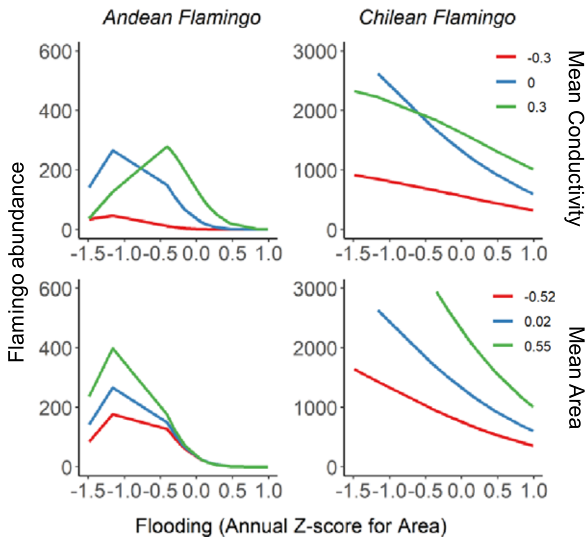

Figure 6. The variation in abundance of each flamingo species, as predicted by the generalised linear mixed models (GLMMs), based on the influence of flooding conditions (Annual Z-score for Area), mean water conductivity (Mean Conductivity), and mean water surface area (Mean Area). To facilitate the visualisation of the results from these three-way GLMMs, two plots are shown for each flamingo species, considering either Flooding and Mean Conductivity or Flooding and Mean Area as explanatory variables. For both Mean Conductivity and Mean Area, three lines represent different values: the 10th percentile (red), median (blue), and 90th percentile (green). See Figure S2 for the results of the GLMMs for each flamingo species.

or avoiding environmental adversities. The Andean Flamingo is a k-selected, long-lived species likely to minimise the energy cost of migration (Schmaljohann et al. 2022), and, based on their memory, may predict the probability that wetlands in the wintering area may not be favourable and therefore choose not to migrate to these areas. Therefore, Andean Flamingos make alternative and complementary use of wetlands on a subcontinental scale, which includes high Andean and Puna wetlands at different altitudes (3,000–4,800 m a.s.l.), and several lowland wetlands (0–2,000 m a.s.l.) (Caziani et al. 2007).

In the lowland areas of central Argentina, the rainfall pattern of the El Niño years is characterised by heavy rains, which strongly impacts the morphological and physical–chemical characteristics of the wetlands (i.e. larger surface area and lower salinity), which in turn affect the supply of food resources (Guerra et al. 2015; Polla et al. 2018). The lower abundance of both flamingo species in the study area during the years of higher water levels could be associated with a reduction in the foraging area where they usually feed (Romano et al. 2005), as well as a variation in food availability (Battauz et al. 2013). In contrast, a higher abundance of Andean Flamingos at Laguna Brava (4,000 m a.s.l.; the eastern slope of the Andes) was recorded after above-normal rainfall, which led to the formation of islands on the lake, resulting in a key factor for the establishment of a nesting colony (Bucher et al. 2000). Thus, the effects of water fluctuations on flamingo abundance likely depend on whether they occur during the breeding or non-breeding season.

Spatial variation in flamingo abundance at Pampa de las Lagunas

Throughout their distribution, both Andean and Chilean flamingos live in wetlands encompassing a wide water salinity range (Caziani and Derlindati 2000; Frau et al. 2015; Hurlbert and Keith 1979; Romano et al. 2008). In the Pampa de las Lagunas study area, Chilean Flamingos were recorded in most wetlands and along a wide water salinity gradient, whereas the Andean Flamingo was recorded in a smaller number of wetlands with intermediate water salinity, being rare in wetlands with very low or very high salinity. A similar pattern has been reported for the high Andes lakes, where the distribution of the Andean Flamingo was patchier than the distribution of the Chilean Flamingo (Frau et al. 2015; Hurlbert and Keith 1979). Differences in the range of wetlands where the species were recorded could be associated with differences in their diets (Polla et al. 2018). The Chilean Flamingo has a wider diet breadth that includes zooplankton, benthic invertebrates, and even seeds, whereas the Andean Flamingo feeds mainly on phytoplankton (Mascitti and Kravetz 2002; Ortiz et al. 2020; Polla et al. 2018; Tobar et al. 2012, 2014). Food availability for the Andean Flamingo could be conditioned by low or high water salinity.

For both flamingo species, there were also differences in wetland use among years based on the drought/flooding status, water salinity, and the size of the wetlands. In very dry years, many wetlands significantly increased their water salinity, some of them to the extreme that no zooplanktonic organisms were recorded, while some small wetlands dried out (Battauz et al. 2013). In these dry years, both flamingo species concentrated in wetlands that most years have the lowest water salinity and are not usually used. In contrast, in very wet years, most areas are flooded, leaving almost no mud shore habitat for foraging, and water salinity markedly decreases, thus reducing the abundance of both flamingo species in most wetlands. However, after three El Niño years with very high precipitation that lowered the water salinity of a large saline lake (Las Tunas), many Chilean Flamingo congregated, and a nesting colony was recorded (Barisón et al. 2018). Thus, wetland use by flamingos depends on the interaction between climate variation and wetland characteristics.

Conservation

The Andean Flamingo has the smallest global population of the six flamingo species, estimated at about 80,000 individuals (Derlindati et al. 2024; Marconi et al. 2020). Our results showed that the abundance of this species showed marked fluctuations during our 15-year study period (2008–2022) in the non-breeding lowlands of Pampa de las Lagunas, ranging from years with about 25% of the world population to other years when no individuals were recorded. These fluctuations were associated with variations in the environmental conditions due to El Niño–La Niña cycles. Thus, conservation strategies should analyse long-term trends in population dynamics and must consider the differential and alternative use that Andean Flamingos make of different wetlands subject to variations imposed by macroclimatic cycles, and particularly in the context of climate change scenarios (Derlindati et al. 2024).

Global climate change raises concerns for flamingo conservation (Delfino 2023). Habitat suitability models predict a high impact of climate change on the future distribution of flamingos. All six extant flamingo species show a wide variation in the gain or loss of suitable habitats, and five will experience a net reduction in suitable areas in the next few decades. These models predict stronger reductions in suitable areas for the Andean Flamingo than for the Chilean Flamingo (Delfino 2023). However, because these models are mainly based on the breeding areas, the Pampa de las Lagunas site is not considered in the predicted distribution maps for the Andean Flamingo, so suitable areas are underestimated. Non-breeding sites are also key for the future of the Andean Flamingo populations because they must provide sufficient high-quality food resources for flamingo survival and subsequent reproductive success in their breeding areas. In addition, they are important for developing pre-reproductive activities like courtship displays and pair formation (Derlindati et al. 2014).

Flamingos are affected by different types of threats (Delfino and Carlos 2024; Derlindati et al. 2024). For the three flamingo species in the Southern Cone, populations are impacted by climate change, industrial-scale mining, unregulated tourism, and pollution, among others in the Altiplano (Gutiérrez et al. 2022; Marconi et al. 2022), and by human activities of various kinds (e.g. agriculture, pumping, urbanisation, unregulated tourism, waste, etc.) in the lowland areas (Romano et al. 2014). The necessity of wetland habitat conservation at the regional level to ensure the existence of alternative sites for feeding and breeding under varying water level–rainfall conditions has been proposed for the Chilean Flamingo (Bucher 1992). Some wetlands in the Pampa de las Lagunas complex are considered key wintering sites for Andean Flamingo conservation (Delfino and Carlos 2024) and are included in the Network of Wetlands for Flamingo Conservation (Marconi and Sureda 2008). This international conservation approach highlights the importance of considering the Andean and Puna Flamingo populations at a regional scale, including highlands and lowlands in Argentina, Bolivia, Chile, and Peru. A broad spectrum of conserved sites across a wide range would contribute to the effective conservation of these flamingo species in the long term, providing spatial and temporal resilience in a rapidly changing environment.

Conclusions

The results of the GLMMs showed higher abundances of both flamingo species in wetlands with intermediate to high water salinity (supporting Hypothesis 1), and an increase in flamingo abundance with wetland size for Chilean Flamingo (partially supporting Hypothesis 2). We found a decrease in the abundance of both flamingo species under higher annual flooding conditions, but a decrease in flamingo abundance in strong La Niña years only for the Andean Flamingo, thus partially supporting Hypothesis 3). In La Niña years, we recorded a higher relative abundance of both flamingo species in wetlands with lower water salinity, but no differences in smaller wetlands, thus supporting Hypothesis 4 but not Hypothesis 5 (Figure 1). Finally, our study carried out for 15 consecutive winters in 24 wetlands showed that Andean Flamingos were present in a narrower salinity range of wetlands, and a narrower range of flooding conditions, thus supporting Hypotheses 6 and 7, respectively.

Our study identified significant impacts of ENSO on annual flooding conditions, wetland size, and wetland water salinity, and thus in the abundance of wintering Andean and Chilean flamingos in lowland wetlands of Argentina. The abundance of the Andean Flamingo was significantly impacted by severe flooding and drought conditions, while the Chilean Flamingo showed more plasticity in its distribution. These different responses are notable given the lower global population numbers and vulnerability of the Andean Flamingo.

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