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Habitat Changes at the Local Scale Have Major Impacts on Waterfowl Populations Across a Migratory Flyway

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ABSTRACT

Migratory waterbirds are experiencing severe declines worldwide due to habitat loss. Their life cycles often span different countries and continents, highlighting the need for safeguarding wetland networks along migratory flyways. However, there are gaps in understanding how changes in specific sites can impact species at the biogeographical scale. Here we used a wetland of international importance (the Guadalquivir marshes, SW Spain) as a case study to investigate the causes and consequences at the flyway scale of annual changes in wintering waterbird assemblages. To do so, we combined 38 years of local and international waterfowl winter counts, environmental and remote sensing data encompassing 432 Ramsar sites, and a functional approach through structural equation modelling (SEM). We show that the environmental conditions experienced by wintering waterfowl in the study area were correlated with changes in their biogeographical populations in the East Atlantic Flyway. We found that during the last 40 years, the waterfowl assemblage wintering at the Guadalquivir marshes has shifted from a community composed mainly by herbivores and pre-Saharan dabbling granivores, to the current one dominated by Trans-Saharan dabbling granivores. Declines in 9/15 of the species studied were associated with the deterioration of the Doñana National Park natural marshes, whereas changes in the remnant six species responded mainly to global factors, such as the increase in winter temperatures in other areas of their distribution range. These results underscore the importance of considering global factors and flyway population data when interpreting regional trends of migratory animals. But also, that changes in specific wetlands can have measurable global impacts. Being that the long-term persistence of migratory animals in a changing world entails the protection and integrity of migratory flyways beyond national borders.

1 | Introduction

Wetlands are one of the most biodiverse and productive ecosystems on Earth (Mitsch and Gosselink 2015). Yet, over 70% of the world's wetlands have been lost in the last century (Davidson 2014), and an additional wetland loss of ~78% is projected by the end of the 21st century (Spencer et al. 2016).

Migratory waterbirds are particularly vulnerable to wetland loss (Maclean et al. 2008; Steen, Skagen, and Noon 2014; Zurell et al. 2018). Their annual life cycles occur throughout a network of wetlands (commonly referred to as flyways), where few sites function as nodes embedded in a matrix of inadequate habitat (Donnelly et al. 2021). Changes in the properties of these nodes can lead to spatiotemporal reconfigurations in the use of sites (Iwamura et al. 2013; Merken et al. 2015; Verhoeven et al. 2018; Pavón-Jordán et al. 2018), potentially impacting survival (Piersma et al. 2016), fitness (Norris et al. 2004; Saino et al. 2004; Alves et al. 2013; Van Gils et al. 2016; López Calderón et al. 2019), and ultimately, population dynamics and distribution (Merken et al. 2015; Piersma et al. 2016, 2017; Studds et al. 2017; Pavón-Jordán et al. 2018; Alves et al. 2019). Regarding this matter, wintering and stopover sites are of particular importance; they can concentrate a substantial fraction of waterbird's biogeographical populations (Rendón et al. 2008; Lourenço et al. 2016; Peng et al. 2017; Oudman et al. 2020). Indeed, migratory strategies can affect individual survival and fitness, as described for several species (Mihoub et al. 2010; Lok et al. 2011; Duriez et al. 2012; Rushing, Marra, and Dudash 2016; Dossman et al. 2022; Peng et al. 2023). However, few studies to date have attempted to integrate local and flyway data to assess the causes and consequences of wintering habitat change on a species' population dynamics at the biogeographical scale (but see Zwarts et al. 2009; Piersma et al. 2016; Piersma et al. 2017). In the current context of profound wetland transformations, it is vital to understand migratory waterbirds responses to habitat change to ensure their long-term persistence and, the integrity of migratory flyways (Merken et al. 2015; Donnelly et al. 2021).

Migration has been often invoked as a resource-tracking mechanism (Herrera 1980; Piersma, Verkuil, and Tulp 1994; Somveille, Rodrigues, and Manica 2015), being temperature and rainfall, some of the main factors governing resource availability (Fei, Liu, and Yali 2017). For instance, green-winged teals (*Anas crecca*) adjust their spring migration in response to ground temperatures encountered on-route (Cerritelli et al. 2023), and north-eastwards shifts in the winter distribution and population trends of waterbirds are correlated with an increase in early winter temperature (Jiguet et al. 2010; Lehikoinen et al. 2013; Pavón-Jordán et al. 2018; Linssen et al. 2023). Regarding this matter, fluctuations of climatic oscillators, such as the North-Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO), have a strong influence on winter and spring weather, impacting breeding success and survival of resident and migratory birds worldwide (Nott et al. 2002; Devney, Short, and Congdon 2009; Gordo, Barriocanal, and Robson 2011; LaManna et al. 2012; Fei, Liu, and Yali 2017). At the local scale, waterbird abundance is also driven by other factors such as habitat quality, availability and connectivity (Gonzalez-Gajardo, Sepúlveda, and Schlatter 2009; Iwamura et al. 2013; Pap et al. 2013; Vanausdall and Dinsmore 2019; Larson, Cordts, and Hansel-Welch 2020; Ballard, Jones, and Janke 2021; Malekian, Salarpour, and Ranaie 2022). Hence, interannual fluctuations in global and local factors experienced by waterbirds throughout their life cycles do affect future breeding success and survival at the flyway scale (Lok et al. 2011; Duriez et al. 2012; Masero et al. 2017; Fei, Liu, and Yali 2017; Rakhimberdiev et al. 2018; Peng et al. 2023) in a non-reversible manner, referred to hereafter as 'carry-over effects' (Senner, Conklin, and Piersma 2015).

The Guadalquivir marshes (GM; SW Spain) display a strategic position as a steppingstone between Africa and Europe within the East Atlantic migratory flyway (EAF). Historically, the GM have been praised for its outstanding waterbird diversity and abundance (Chapman and Buck 1893; Chapman and Buck 1910; Mountfort and Ferguson-Lees 1959), being a Ramsar and UNESCO World Heritage Site and meeting international importance criteria for at least 25 waterbird species (Máñez et al. 2010; Green et al. 2016), while also containing close to or more than 10% of the biogeographical population for six waterbird species (Rendón et al. 2008). Although c. 30,000 ha of natural marshes within the GM are currently protected under Doñana National Park, the GM faced an extensive transformation over the past century: more than 80% of its surface area was converted into agriculture (mainly rice fields) and semi-extensive aquaculture ponds, and its hydrological regime shifted to an almost entirely rain-dependent wetland. Furthermore, groundwater overexploitation for agriculture and tourism is responsible for desiccating waterbodies all over Doñana National Park (de Felipe, Aragonés, and Díaz-Paniagua 2023). All this, together with a long ongoing drought resulted in an abrupt decline in natural and man-made wetlands, raising a wide international concern about the fate of the GM and its unique biodiversity (Navedo et al. 2022; Camacho et al. 2022; Santamaría and Martin-Ortega 2023; Vansteelant 2023; Green et al. 2024).

Although some previous works analysed the numerical trends experienced by waterbirds in the GM (Rendón et al. 2008; Máñez and Arroyo 2014), these studies did not consider the role of climatic and environmental factors on waterbird assemblages. Regarding this matter, Almaraz and Amat (2004) studied the effects of climatic oscillators on the spatiotemporal patterns of the white-headed duck (*Oxyura leucocephala*) in southern Spain. However, we are unaware of any study attempting to integrate both local and global data to investigate how waterfowl winter abundance might respond to environmental factors, and whether changes in this single but key wetland can have measurable carry-over effects on waterfowl populations at the flyway scale.

Since 1980, the GM have been subject to standardised monthly waterbird counts. These counts, coupled with the well-documented transformations, pose an excellent opportunity to use the GM as a case study to explore the causes and consequences of interannual changes in wintering waterbird assemblages at the flyway scale, while also serving as valuable guidance for policymakers in making informed management decisions in a critical moment for the fate of this iconic and threatened wetland. To do so, we used a functional approach and structural equation modelling (SEM). We employed a comprehensive dataset spanning 38 years (1984/85–2021/22), which includes both local and international winter waterfowl counts and remote sensing data of 432 Ramsar sites along the East Atlantic migratory Flyway. Our specific aims were to: (i) assess the long-term trends experienced by wintering waterfowl within the Guadalquivir delta; (ii) evaluate the role of local and global factors on the interannual differences in waterfowl assemblages within the GM; and (iii) assess the presence and magnitude of carry-over effects of wintering conditions within the GM on waterfowl populations along the East Atlantic flyway.

Specifically, we hypothesise that waterfowl winter abundances at the GM will vary in response to changes in local and global environmental conditions. We expect these effects to differ among waterfowl functional groups, based on their habitat and diet preferences. Furthermore, considering the international significance of the GM as a wintering site, we predict that changes in wintering conditions at the GM will have carry-over effects on waterfowl populations throughout the East Atlantic flyway on the following year.

2 | Materials and Methods

2.1 | Study Area

Our study area comprises the marshes of the Guadalquivir River estuary (SW Spain). Although this wetland originally covered up to 180,000 ha of untransformed habitats in the early 19th century, subsequent land transformations have diminished its size to the current matrix of natural marshes, agricultural lands (mainly cereals, including extensive rice fields), extensive aquaculture ponds and salt pans (Figure 1).

Within the Guadalquivir Marshes, the untransformed area nowadays covers 32,000 ha of natural, strictly protected marshes under the Doñana National Park (Doñana marshes, hereafter). Several rivers and streams fed these marshes in the past but were channelised during the second half of the 20th Century, which transformed the area to an alluvial marsh almost entirely dependent on rainfall, although still receiving water input from a reduced number of temporary streams. The climate in the area is Mediterranean, with mild winters (mean winter temperature: 10.89°C ± 1.71 SD) and warm summers (mean summer temperature: 23.53°C ± 2.06 SD). Annual precipitation (measured from 1 September of 1 year to 31 August of the following year) is highly variable, with a 568.2 mm (±199 SD) annual average, ranging from 169 mm (year 2004–2005) to 1027 mm (year 1995–1996), and 80% of rainfall being concentrated in October–March (de Felipe, Aragonés, and Díaz-Paniagua 2023). Marsh flooding thus follows the same unpredictable pattern of variation that of precipitation in the area.

Surrounding the protected area of the park, up to 37,000 ha of rice paddies may be cultivated every year, representing the main crop in the GM. Rice fields are flooded in May–June and harvested in September–October. However, rice cover changes every year, based on water concessions granted by the Guadalquivir River authority. Traditionally, local hunters left a few paddies flooded during winter to attract waterbirds. Since the early 2000s, the European Commission has encouraged local farmers to adopt agri-environmental schemes to mitigate the impact of agriculture on biodiversity, compensating farmers for keeping the paddies flooded in winter. This practice increased substantially the flooded area available for migratory waterbirds in rice fields.

During the early 1990s, 3200 ha of natural marshes were transformed into an extensive and semi-extensive fish farm complex. The fish farm uses brackish, estuarine water to ensure a permanent or semi-permanent water regime on 45 fishponds of 70 ha. It harbours important waterfowl numbers (Máñez and Arroyo 2014), and in dry years, it can represent along with rice fields the only water bodies available for wintering waterbirds at their arrival in autumn.

Moreover, up to 1500 ha of salt pans and its surrounding areas may be flooded each winter because of heavy rainfall and operations for commercial salt extraction. Yet, Rendón et al. (2008) showed a relatively stable flooded area of these salt pans within and between years.

Thus, the term 'Guadalquivir marshes' (GM) is used hereafter to refer to both transformed and natural lands occurring on the Guadalquivir estuary, which includes the four aforementioned well-differentiated wetland habitats: the Doñana marshes, rice fields, fish ponds and salt pans.

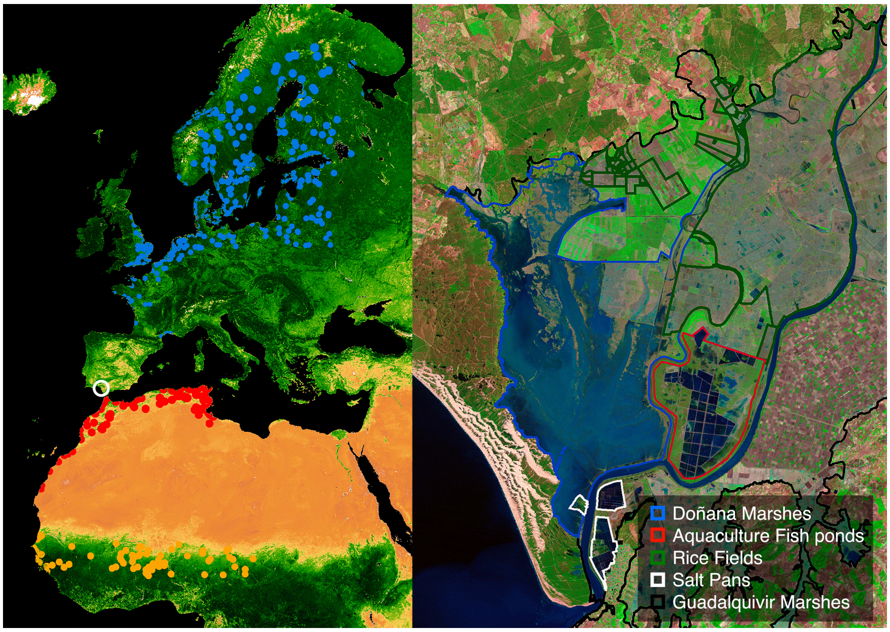


FIGURE 1 | Left: MODIS NDVI-coloured image. White circle marks the Guadalquivir marshes. Orange, red and blue dots denote Ramsar sites belonging to Sahel, North Africa and Europe (respectively) whose climate from 1985 to 2022 was analysed. Right: Detailed view of the study area from a Landsat picture taken on 18 February 1997. Blue outline notes the Doñana marshes; red outline, aquaculture fish ponds; green outline, rice fields; white outline, salt pans; black outline, limit of the Guadalquivir marshes at the beginning of the 20th Century.

2.2 | Waterfowl Surveys

We studied 15 waterfowl species (14 Anatidae and a Rallidae) regularly wintering in the Guadalquivir marshes. Namely, the greylag goose (*Ans anser*), northern pintail (*Anas acuta*), green-winged teal (*A. crecca*), mallard (*A. platyrhynchos*), common pochard (*Aythya ferina*), tufted duck (*A. fuligula*), ferruginous duck (*A. nyroca*), Eurasian wigeon (*Mareca penelope*), gadwall (*M. strepera*), marbled teal (*Marmaronetta angustirostris*), red-crested pochard (*Netta rufina*), white-headed duck (*Oxyura leucocephala*), northern shoveler (*Spatula clypeata*), common shelduck (*Tadorna tadorna*) and common coot (*Fulica atra*). Altogether, these 15 species represent 65% of all waterbirds counted in the GM (Máñez and Arroyo 2014).

The vast expanse of the GM, coupled with the difficult access to certain areas during the flooding period, may render aerial waterfowl census as an alternative to traditional ground techniques for assessing the population size of conspicuous aquatic birds throughout the year (Tamisier and Dehorter 1999). Aerial bird counts were performed using a light aircraft (e.g., CESSNA high-wing) on a monthly basis throughout the whole period of study by three experienced observers from the Natural Processes Monitoring Team (ICTS-RBD) from the Doñana Biological Station (EBD-CSIC). We used the annual winter maximum count from 1984/1985 to 2021/2022 for 12 of the waterfowl species. Aerial census is however unsuitable for rare and not easily distinguishable species, such as *A. nyroca*, *M. angustirostris* and *O. leucocephala*, for which we employed terrestrial counts. We used the ICTS-RBD monitoring database to gather abundances of each species from 1984/1985 to 2002/2003. For each species and winter, we summed all birds counted in different areas of the GM during any given week and retained the maximum in any week as the winter maximum count. From 2002–2003 to 2021–2022, terrestrial counts were standardised following Máñez and Arroyo (2014). We combined both sources of information and confirmed that the year of overlap (2002–2003) produced similar results.

International annual data on waterfowl population sizes in the Western Palearctic were obtained from the International Waterbird Census (IWC-Wetlands International). This is a global monitoring programme that collects information about the numbers of wintering waterbirds in wetland sites since 1967 (see Wetlands International, 2022 for more details on geographic, temporal cover and methodology). Considering that not all waterfowl breeding in Europe winter nor migrate through the Iberian Peninsula, we used the Atlas of Anatidae Populations in Africa and Western Eurasia (Scott and Rose 1996) and complemented it with bird ringing data to only consider counts from countries where ducks winter in the GM. Ringing information was obtained using historical (1910–2022) files from the Aranzadi Society of Sciences (https://www.aranzadi.eus/oficina-anillamiento), ICTS-RBD (http://anillamiento.ebd.csic.es) and the Spanish Ornithological Society (SEO/Birdlife 2022) ringing offices.

2.3 | Remote Sensing Data

The study used atmospherically corrected Landsat 5, 7 and 8 surface reflectance images available for the GM in the Google Earth Engine (GEE) platform, which covered from April 1984 to March 2022. We removed images with > 20% cloud cover and applied a cloud mask to the remaining images to only retain pixels classified as clear. We used Landsat's embedded quality assessment band (QA pixel), which uses multiple spectral bands and thresholds to identify clouds and cloud shadows. The resulting filtered image collection composed of 609 images was used for subsequent analysis.

Landsat's band 5 (wavelength: 1.55–1.75 μm) has been successfully used to detect the flooded or dry state of shallow, turbid waters that often present emergent vegetation (Bustamante, Aragonés, and Afán 2016; Díaz-Delgado et al. 2016). We visually inspected and selected a threshold value for the image collection, where pixels with standardised band 5 reflectance values below 0.128 on a given date were identified as flooded. We extracted the winter-flooded area for each habitat (either Doñana marshes, rice fields, fish ponds and salt pans) and hydrological year as an index of habitat availability. We also accounted for potential legacy effects of maximum flooded area of the Doñana marshes and rice field cover during the previous spring.

Primary production is known to impact waterbird breeding success by modulating arthropod abundance (Silva-Monteiro et al. 2022). The Normalized Difference Vegetation Index (NDVI) is a cost-effective estimate commonly used to measure primary productivity from satellite imagery. By calculating the ratio between the red (0.77–0.90 μm) and near-infrared (0.63–0.69 μm) bands, the NDVI quantifies vegetation greenness, with higher values meaning 'greener' and therefore, productive areas. We used the NDVI as a proxy of plant biomass in non-flooded areas of the Doñana marshes during winter, as flooded areas may constitute open, often turbid waters that could bias NDVI estimates. Bulrush reedbeds (composed of *Bolboschoenus maritimus* and *Schoenoplectus litoralis*) represent the most abundant and widespread helophytes in the Doñana marshes. Their seeds and nutritious rhizomes often represent the main food for herbivore and granivore waterbirds (Amat, García-Criado, and García-Ciudad 1991; Figuerola et al. 2010). We considered potential effects of bulrush productivity on waterfowl abundance by using its mean NDVI during spring (when its vegetative growth peaks; Amat 1995). Moreover, phytoplankton represents the main food source for zooplankton, upon which several waterbirds feed. We thus accounted for a potential indirect effect of phytoplankton abundance by calculating the winter mean NDVI of the fish ponds and the salt pan's flooded area.

Landsat's near-infrared band (0.63–0.69 μm) has been used in the past to predict water turbidity of the Doñana marshes. Following the procedure described in Bustamante et al. (2009), we used winter's mean values of the near-infrared band to extract the mean winter turbidity of the Doñana marshes.

2.4 | Meteorological Data

Based on our knowledge of the area, the Doñana marshes begin to flood once cumulated rainfall surpasses 200 mm. We considered the 'flood date' as the day of the year (counting from 1 September) when the cumulated rainfall surpassed the 200 mm threshold in each hydrological cycle. Daily precipitation in autumn and winter, together with mean winter temperature, was obtained from a meteorological station located within the Doñana National Park (https://meteorologia-palacio.icts-donana.es).

We used the ERA5 dataset (Hersbach et al. 2023) and GEE to obtain historical (1984–2022) data on mean autumn temperature and accumulated rainfall for 432 Ramsar sites (Figure 1) distributed along the Sahel (17.5° N—7.5° N; $n = 71$), North Africa (36.7° N—18.3° N; $n = 64$) and the European section of the East Atlantic flyway ($n = 297$). ERA5 is a dataset provided by the Copernicus Climate Change Service (C3S) that offers monthly mean estimates of single-level atmospheric variables. It is a reanalysis dataset that combines observational data from various sources with a numerical weather prediction model to provide comprehensive and consistent information on climate conditions at a global scale (Hersbach et al. 2020). We created a 20 km-radius buffer around Ramsar site centroids and extracted, for each region (either Sahel, North Africa or Europe) and year the mean temperature, and accumulated rainfall from 1 September to 30 November. The North-Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO) are also known to affect population dynamics of waterbirds in the northern hemisphere (Almaraz and Amat 2004; Gordo, Barriocanal, and Robson 2011). We considered the mean values of NAO and ENSO during winter (December, January and February, when waterfowl abundance peaks), which were obtained from the Climate Prediction Center of the National Oceanic and Atmospheric Administration (NCEI 2023).

2.5 | Functional Traits

We examined the existing literature and historical duck ringing/recovering data from the Aranzadi Society of Sciences (https://www.aranzadi.eus/oficina-anillamiento), ICTS-RBD (http://anillamiento.ebd.csic.es) and the Spanish Ornithological Society (SEO/Birdlife 2022) to gather information regarding diet, foraging specialisation and migratory behaviour for the 15 waterfowl species studied (Table S1). Diet data searches prioritised studies analysing gut (oesophagus/crop and gizzard) content's dry weight, undertaken in autumn–winter in the Mediterranean region and in a similar habitat to the matrix of natural, transformed and cultivated marshes which can be found in our study area. Foraging behaviour of *A. anser*, *A. acuta*, *A. crecca*, *A. platyrhynchos*, *A. ferina*, *A. fuligula*, *M. strepera*, *M. penelope*, *N. rufina* and *S. clypeata* were extracted from Amat (1980, 1984), Amat, García-Criado, and García-Ciudad (1991) and completed for *A. nyroca*, *F. atra*, *M. angustirostris*, *O. leucocephala* and *T. tadorna* using the same premises as for diet data (Table S1).

Based on a dimensionality reduction approach (Figure S1) on such characters, we identified eight distinct functional groups: (1) herbivores, which encompassed waterfowl with > 70% of their diet consisting of plant material (*A. anser*, *F. atra*, *M. strepera* and *M. Penelope*); (2) pre-Saharan dabbling granivores: granivore (> 80% of diet consisting of seeds) waterfowl feeding on the water surface or in very shallow water (< 10 cm) and whose southernmost wintering quarters are in North Africa (*A. crecca and A. platyrhynchos*); (3) trans-Saharan dabbling granivores: granivores feeding on the water surface or shores and having their southernmost wintering quarters in Sahelian wetlands (*A. acuta* and *S. clypeata*); (4) generalist granivores: granivores facultatively using any foraging strata (*A. nyroca* and *M. angustirostris*); (5) carnivorous divers: waterfowl specialised in diving (> 80% of foraging time) and feeding on aquatic invertebrates (> 90% of diet) (*A. fuligula*); (6) omnivorous divers: diving waterfowl facultatively feeding on invertebrates, plant material and seeds (*O. leucocephala*); (7) herbivorous divers: diving waterfowl feeding mainly on seeds and plant material (*A. ferina* and *N. rufina*); and (8) generalist omnivores: waterfowl facultatively feeding on invertebrates, plant material and seeds in any given foraging strata (*T. tadorna*).

2.6 | Statistical Analyses

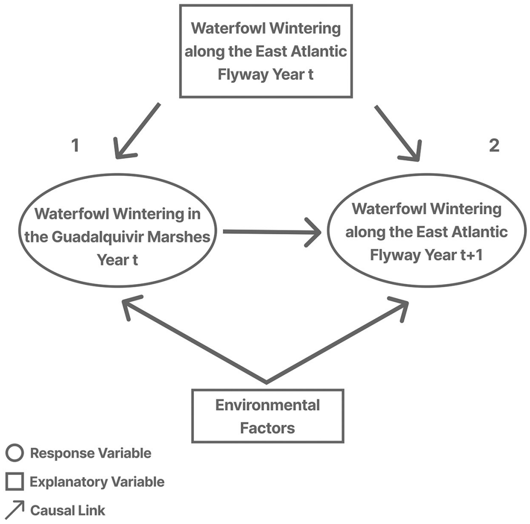
All statistical analyses were performed in the R environment (Version 1.2.5033; R Core Team 2021). No variables were removed prior to the statistical analyses, as Farrar–Glauber tests (F–G test) and variance inflation factors (VIF) showed that there were no collinearities.

We employed a SEM approach to disentangle the role of environmental factors on wintering waterbird abundance and population trends at the local and flyway scale. SEM is a probabilistic modelling technique that postulates a causal network involving multiple variables that can function as both predictors and response variables. Specifically, we used confirmatory path analysis, also known as piecewise SEM, drawing upon concepts from graph theory. In piecewise SEM, the path diagram is translated into a system of linear equations, such as linear mixed models, enabling the evaluation of each equation individually and accommodating diverse distributions and sampling designs. Furthermore, the overall adequacy of the causal network can be assessed using a directed separation test, commonly referred to as the 'd-separation test'. This test examines the assumption of conditional independence among all variables, ensuring that no missing relationships exist among unconnected variables (Shipley 2016).

We developed a different path model for each one of the eight functional groups studied, each of them composed of two linear mixed models whose response variables were the log-transformed annual maximum winter count in the GM and the EAF, respectively. The first model tested the effect of local and global environmental factors on winter abundance of waterfowl in the GM (Figure 2). The second model tested the effect of local and global environmental factors on waterfowl population size in the East Atlantic Flyway on the next year (Figure 2). Up to 24 environmental variables were considered. Although each model contained a different subset of response variables based on the functional group's natural history (Figure 2), the selected variables were as follows: the log-transformed maximum winter counts in the GM for every species in year t, log-transformed maximum winter counts in the EAF for every species in year t, log-transformed maximum winter counts in the EAF for every species in year $t+1$, flooded area at the Doñana marshes, Doñana marshes' NDVI, flood date of the Doñana marshes, turbidity, spring-flooded area at the Doñana marshes, bulrush productivity, rice field cover, rice field flooded area, fish pond flooded area, fish pond NDVI, salt pan flooded area, salt pan NDVI, precipitation and winter mean temperature in the GM, mean autumn temperature in European, North African and

Glossary of Variables Considered

Variable	Description
max count GM	Maximum count of waterfowl in the Guadalquivir marshes in a given year
max count EU in t	Maximum count of waterfowl in the East-Atlantic Flyway in year t
max count EU in t + 1	Maximum count of waterfowl in the East-Atlantic Flyway in year t + 1
Winter Flooded Area	Winter flooded area of the Doñana marshes
Winter NDVI	Winter NDVI value of the Doñana marshes
Flood Date	Day of the year that accumulated rainfall surpassed 200 mm
Turbidity	Water turbidity of winter flooded area
Temperature	Mean winter temperature
Rainfall	Autumn and winter accumulated rainfall
Spring Flooded Area	Maximum flooded area of the Doñana marshes in the previous hydrological cycle
Bulrush Productivity	NDVI value of bulrush reedbeds in the previous hydrological cycle
Rice Field Cover	Area of rice fields cultivated in the previous hydrological cycle
Rice Fields Flooded	Winter flooded area of rice fields
Fish Pond Flooded Area	Winter flooded area of fish ponds
Fish Pond NDVI	Winter NDVI value of fish ponds
Salt Pan Flooded Area	Winter flooded area of salt pans
Salt Pan NDVI	Winter NDVI value of salt pans
EU Temperature	Autumn temperature in European Ramsar sites
NA Temperature	Autumn temperature in north African Ramsar sites
SA Temperature	Autumn temperature in Sahelian Ramsar sites
NA Rainfall	Autumn rainfall in north African Ramsar sites
SA Rainfall	Autumn rainfall in Sahelian Ramsar sites
NAO	Winter mean of North Atlantic Oscillation
ENSO	Winter mean of El Niño Southern Oscillation



Response variable	Explanatory Variable	Functional Groups	Response variable	Explanatory Variable	Functional Groups
1. max count GM in t	*max count EU in t*	1, 2, 3, 4, 5, 6, 7, 8	**2. max count EU in t + 1**	*max count EU in t*	1 ,2, 3, 4, 5, 6, 7, 8
	Winter Flooded Area	1, 2, 3, 4, 5, 6*, 7, 8*		*max count GM in t*	1, 2, 3, 4, 5, 6, 7, 8
	Winter NDVI	1*, 2, 3*, 4*, 5*, 6, 7*, 8*		*Winter Flooded Area*	1, 2, 3, 4, 5, 6, 7, 8*
	Flood Date	1, 2, 3, 4, 5, 6, 7,		*Winter NDVI*	1*, 2*, 3*, 4*,
	Turbidity	1, 2, 3, 4, 5, 6*, 7, 8		*Flood Date*	1, 5, 6, 7,
	Temperature	2, 3, 4, 5, 6, 7, 8		*Turbidity*	1, 4, 5, 6, 8
	Rainfall	4, 5, 8		*Temperature*	1, 2, 3, 4, 5, 6, 7, 8
	Spring Flooded Area	1, 2, 3, 4, 6*, 8*		*Rainfall*	4, 5, 8
	Bulrush Productivity	2*, 3*, 4*, 6*,		*Spring Flooded Area*	1, 2, 3, 4, 6,
	Rice Field Cover	1, 2, 3, 4, 5, 6*, 7, 8		*Bulrush Productivity*	1*, 2*, 3*, 4*, 5*, 6, 7,
	Rice Fields Flooded	1, 2, 3, 4, 5, 6*, 7, 8		*Rice Field Cover*	1, 2, 3, 4, 5, 6, 7, 8
	Fish Pond Flooded Area	1, 2, 3, 4, 5, 6, 7, 8		*Rice Fields Flooded*	1, 2, 3, 4, 5, 6, 7, 8
	Fish Pond NDVI	5, 7, 8		*Fish Pond Flooded Area*	1, 2, 3, 4, 5, 6, 7, 8
	Salt Pan Flooded Area	8		*Fish Pond NDVI*	5, 7, 8
	Salt Pan NDVI	8*		*Salt Pan Flooded Area*	8
	EU Temperature	1, 2, 3, 5, 7, 8		*Salt Pan NDVI*	8
	NA Temperature	1, 2, 3, 4, 5, 7, 8		*EU Temperature*	2, 3, 5, 7, 8
	SA Temperature	3,		*NA Temperature*	4, 8
	NA Rainfall	1, 2, 3, 4, 5, 6, 7, 8		*NA Rainfall*	1, 3, 4,
	SA Rainfall	3,		*NAO*	1, 2, 3, 4, 5, 6, 7, 8
	NAO	1, 2, 3, 4, 5, 6, 7, 8		*ENSO*	1, 2, 3, 4, 5, 6, 7, 8
	ENSO	1, 2, 3, 4, 5, 6, 7, 8			

1. Herbivores; 2. Pre-Saharan dabbling granivores; 3. Trans-Saharan dabbling granivores; 4. Generalist granivores;
5. Carnivorous divers; 6. Omnivorous divers; 7. Herbivorous divers; 8. Generalist omnivores
* Square-root transformed variable

FIGURE 2 | Upper left corner: Name and description of the environmental variables considered in the SEM. Upper right corner: Causal flow network structure of the SEM constructed for each waterfowl functional group. Down: Model structure of the SEM considered for each functional group. Functional Groups' column denotes the waterfowl groups for which a variable was included in the SEMs.

Sahelian Ramsar sites, autumn precipitation in North African and Sahelian Ramsar sites, and winter values of NAO and ENSO. We included the species and the observer as random effects in all functional groups to control for among-species and among-observer effects. Moreover, populations at the biogeographical scale (such as the EAF) can be considered nearly closed populations, where population size at time $t+1$ is likely correlated with that at time t. Thus, we included EAF population size in year t as an explanatory variable for population size at $t+1$. Wintering waterfowl abundance in the GM exhibited temporal autocorrelation only for herbivores, which we accounted for by incorporating an autoregressive correlation structure. Thus, the structure of our SEMs was based on previous knowledge not only on the ecology of the study species but also on hypotheses to be tested (Figure 2). For instance, Sahelian environmental variables are expected to affect only trans-Saharan waterfowl, whereas autumn temperature in Europe was expected to have no effect on waterfowl with a Mediterranean distribution.

The models provided a robust fit to the data and supported the proposed hierarchical structure (herbivores: Fisher's C=13.17, df=16, $p=0.66$; pre-Saharan dabbling granivores: Fisher's C=12.41, df=8, $p=0.13$; trans-Saharan dabbling granivores: Fisher's C=12.39, df=10, $p=0.26$; generalist granivores: Fisher's

C = 12.64, df = 18, p = 0.81; carnivorous divers: Fisher's C = 35.18, df = 26, p = 0.11; omnivorous divers: Fisher's C = 21.32, df = 28, p = 0.81; herbivorous divers: Fisher's C = 33.06, df = 24, p = 0.10; generalist omnivores: Fisher's C = 5.48, df = 6, p = 0.48). The visual inspection of diagnostic plots (e.g., quantile-quantile plots) also indicated a good fit to the data. We conducted the confirmatory path analyses using the package piecewiseSEM (Lefcheck 2016) and linear mixed models with the package nlme (Pinheiro et al. 2023).

3 | Results

Since 1984, an annual average of 295,785 waterfowl (±127,901 SD) used the Guadalquivir marshes as a wintering site. *S. clypeata* was the most abundant species (with an annual average of 77,295 wintering individuals; ±45,838 SD), followed by *A. anser* (50,429 ± 18,503), *A. crecca* (41,465 ± 38,220) and *M. penelope* (39,413 ± 29,599). *A. nyroca* was the scarcest wintering species (5 ± 3), followed by *A. fuligula* (62 ± 102) and *O. leucocephala* (197 ± 195). Overall, herbivores, pre-Saharan and trans-Saharan dabbling granivores accounted for 95.8% of all wintering waterfowl in the GM.

Herbivores, pre-Saharan dabbling granivores, generalist granivores and carnivorous divers experienced negative trends during the study period, whereas trans-Saharan dabbling granivores, omnivorous divers and generalist omnivores showed positive temporal trends (Figure 3). These changes resulted in a reduction of wintering waterfowl abundances in the GM (Figure 4A), and a shift from a community composed of herbivores and pre-Saharan dabbling granivores, to the current one dominated by trans-Saharan dabbling granivores (Figure 4A). There were concurrent changes in wintering habitat composition at the GM. Thus, despite not finding a clear trend in the overall flooded area, the natural marshes experienced a reduction in their winter-flooded area, whereas rice fields experienced the opposite pattern (Figure 4B).

SEMs revealed correlations between the environmental conditions at the Guadalquivir marshes and wintering waterfowl assemblages. But also, that environmental conditions experienced by waterfowl at the GM were correlated to changes in waterfowl populations at the flyway scale (S2). However, the strength and direction of these effects varied for the different functional groups considered.

3.1 | Environmental Correlates in the Guadalquivir Marshes

Both, trans- and pre-Saharan dabbling granivores' winter abundances at the GM responded positively to marsh flooded area

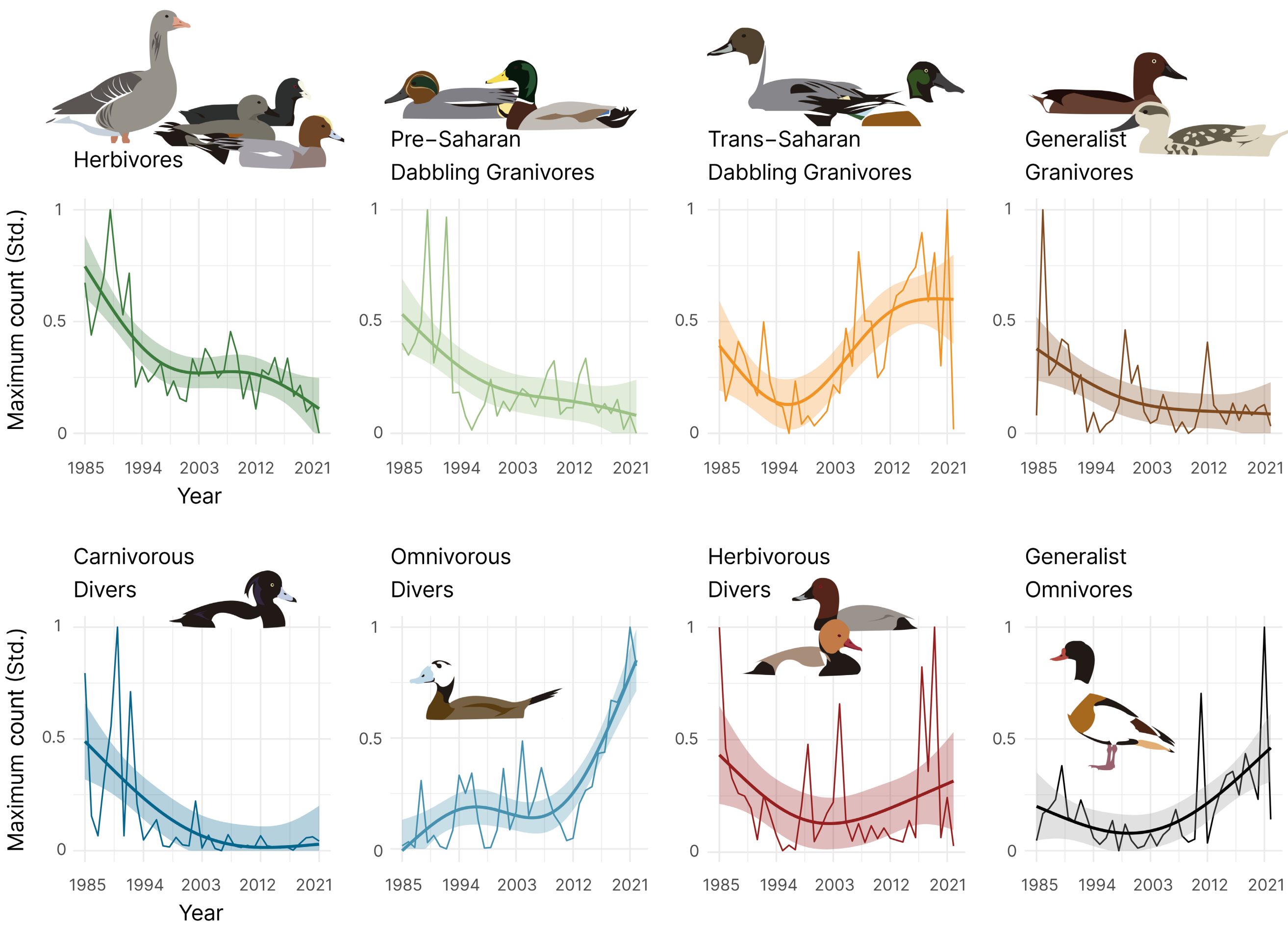


FIGURE 3 | Long-term trends experienced by waterbirds wintering in the Guadalquivir marshes from 1985 to 2022, split by functional groups. Smoothed lines and shaded areas represent GAM smoothed trends and its standard error, respectively.

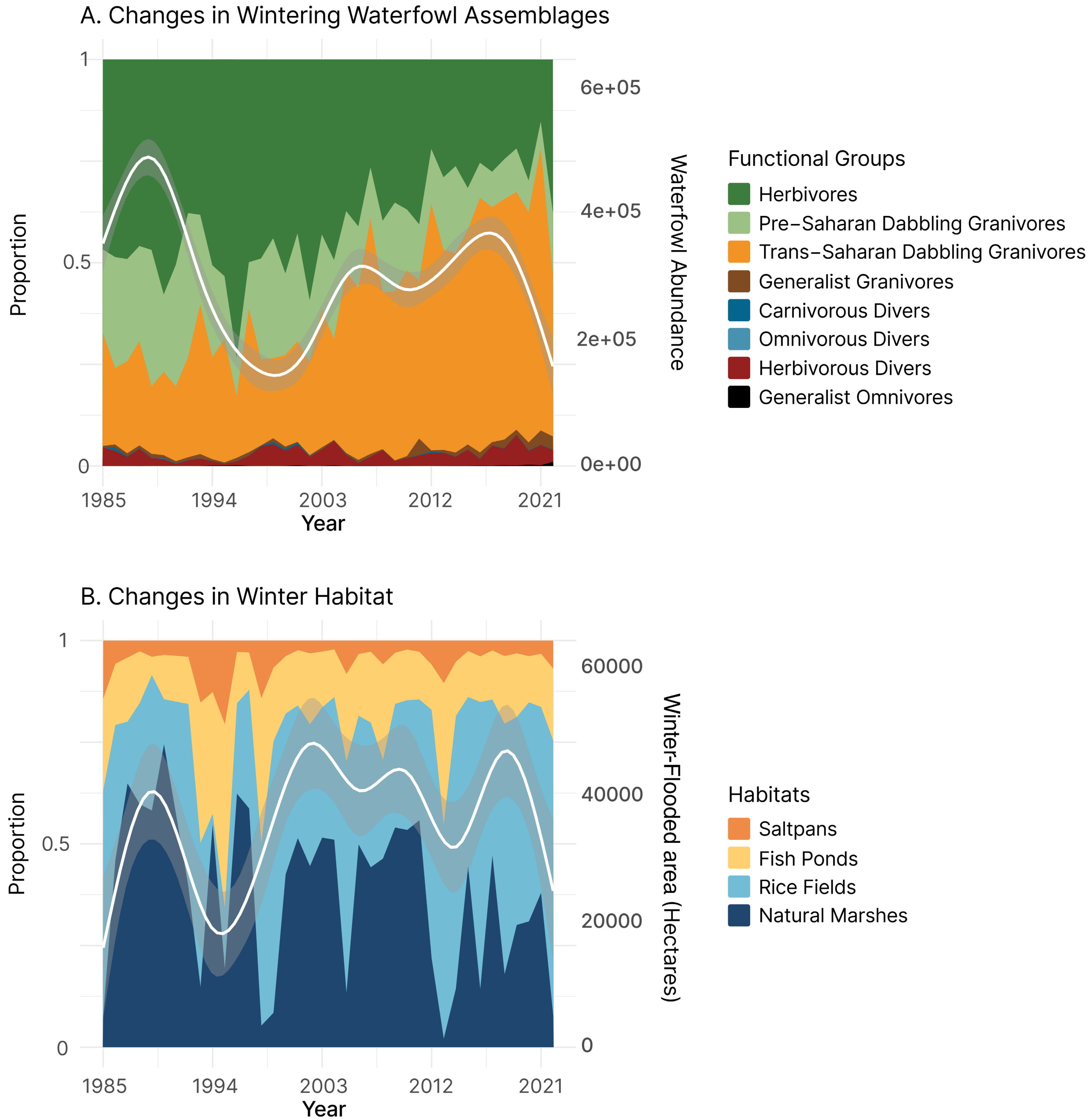


FIGURE 4 | (A) Changes in the wintering waterfowl assemblages in the Guadalquivir marshes from 1985 to 2022, split by functional groups. The white smoothed line and its shaded area represent the loess smoothed trend of annual maximum waterfowl abundance (in number of birds) and its standard error, respectively. (B) Changes in the contribution of each habitat to winter-flooded area within the Guadalquivir marshes from 1985 to 2022. The white smoothed line and its shaded area represent the loess smoothed trend of annual maximum flooded area during winter (in hectares) and its standard error, respectively.

(Std. Est. = 0.79; 0.90, respectively) and negatively to marsh NDVI (Std. Est. = −0.48; −0.56, respectively). Pre-Saharan dabbling granivores also showed a negative response to flooding date (Std. Est. = −0.22) and turbidity (Std. Est. = −0.34). Namely, earlier dates of flooding and lower turbidity levels were associated with larger numbers of mallards and green-winged teals wintering at the GM (Figure 5). Trans-Saharan dabbling granivores responded positively to temperature in European Ramsar sites (Std. Est. = 0.36) and negatively to turbidity (Std. Est. = −0.68), rice field cover (Std. Est. = −0.57) and precipitation in North Africa (Std. Est. = −0.54). More specifically, lower precipitation values in North African Ramsar sites were associated with higher winter counts of *A. acuta* and *S. clypeata* in GM. Generalist omnivores responded negatively to marsh NDVI values (Std. Est. = −0.85) and mean temperature (Std. Est. = −0.77), whereas temperature in North African Ramsar sites (Std. Est. = 0.62) and population

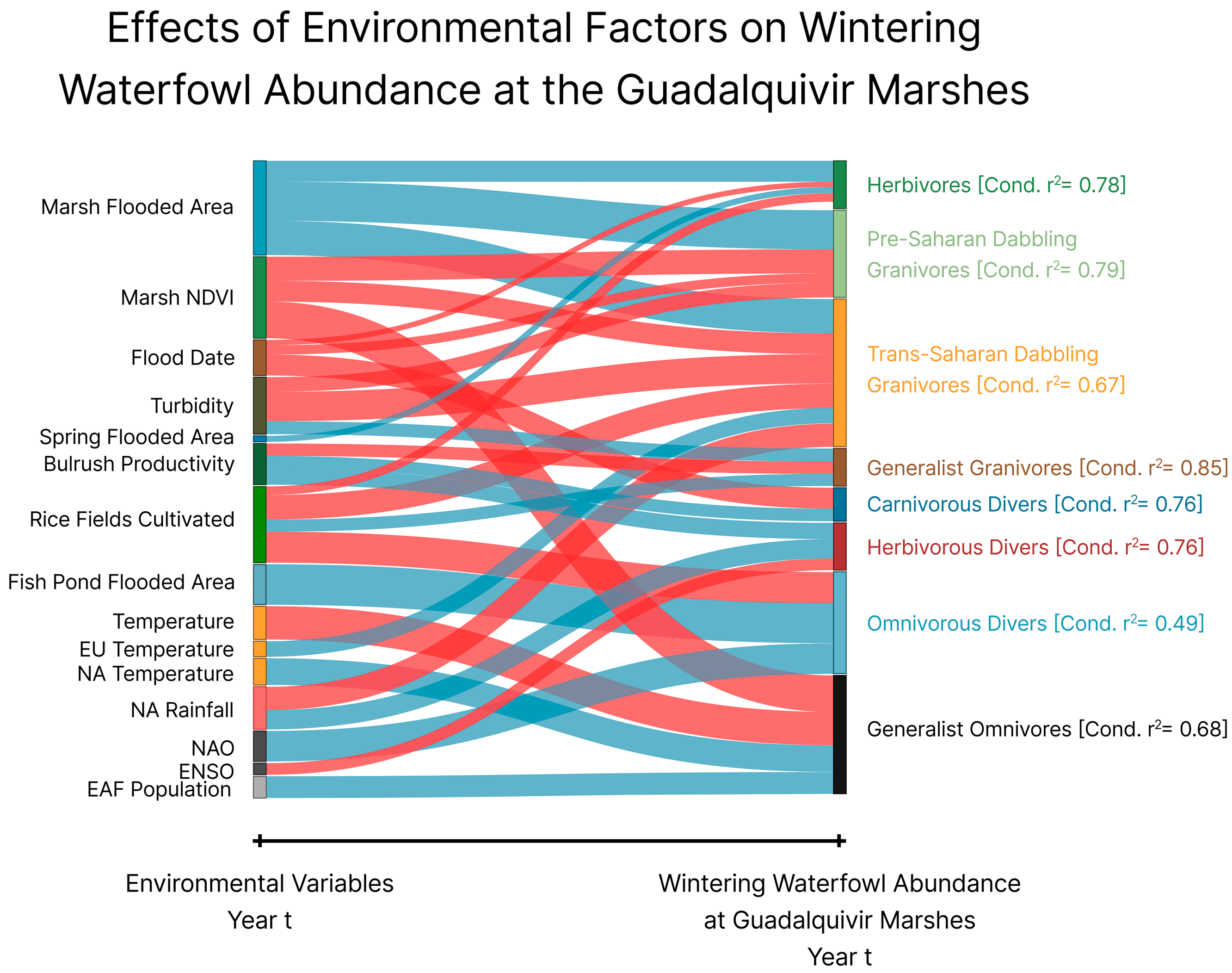


FIGURE 5 | Flow diagram depicting SEM significant standardised estimates of local and global factors explaining interannual changes of wintering waterfowl in the Guadalquivir marshes, split by functional groups. Red links denote negative effects, whereas blue links depict positive ones. Link width is represented relative to the size of the effect. Conditional r-squared values of SEM for each functional group are indicated in brackets.

size at the EAF (Std. Est. = 0.50) had a positive effect on wintering numbers of generalist omnivores in the GM.

Herbivores at the GM responded positively to marsh flooded area (Std. Est. = 0.31). Herbivores were also negatively affected by the flood date (Std. Est. = −0.09), and rice field cover (Std. Est. = −0.18), whereas spring-flooded area showed positive effects on herbivore's winter abundance (Std. Est. = 0.13). Generalist granivores responded positively to turbidity (Std. Est. = 0.30) and rice field cover (Std. Est. = 0.28), whereas bulrush productivity had negative effects (Std. Est. = −0.68).

Regarding diving waterfowl, herbivorous divers responded negatively to ENSO (Std. Est. = −0.27) and positively to precipitation in North African Ramsar sites (Std. Est. = 0.45) and bulrush productivity (Std. Est. = 0.37). Carnivorous divers responded positively to bulrush productivity (Std. Est. = 0.29) and negatively to flood date (Std. Est. = −0.48). On the contrary, omnivorous divers responded negatively to rice field cover (Std. Est. = −0.72) and positively to fish pond flooded area (Std. Est. = 0.94) and NAO index values (Std. Est. = 0.70).

3.2 | Correlates at the Flyway Scale

Our models revealed that EAF's waterfowl abundance in year t was the main factor determining EAF's waterfowl abundance in year $t+1$ (Figure 6). However, the conditions experienced at the GM had significant effects on six out of the eight functional groups analysed.

Pre-Saharan dabbling granivore EAF populations in $t+1$ were positively affected by winter and spring-flooded areas in the Doñana marshes (Std. Est. = 0.31; 0.23), but negatively affected by winter NDVI in the Doñana marshes (Std. Est. = −0.21). Trans-Saharan dabbling granivore EAF populations were positively affected by spring-flooded area (Std. Est. = 0.51) and negatively affected by rice field cover (Std. Est. = −0.35). Spring-flooded area also had positive carry-over effects on herbivores (Std. Est. = 0.09) and diving herbivores (Std. Est. = 0.61) EAF populations. Moreover, mean temperature (Std. Est. = −0.06), temperature at European Ramsar sites (Std. Est. = 0.07) and precipitation in North Africa (Std. Est. = 0.06) also had a significant effect on herbivore EAF populations on $t+1$. Generalist

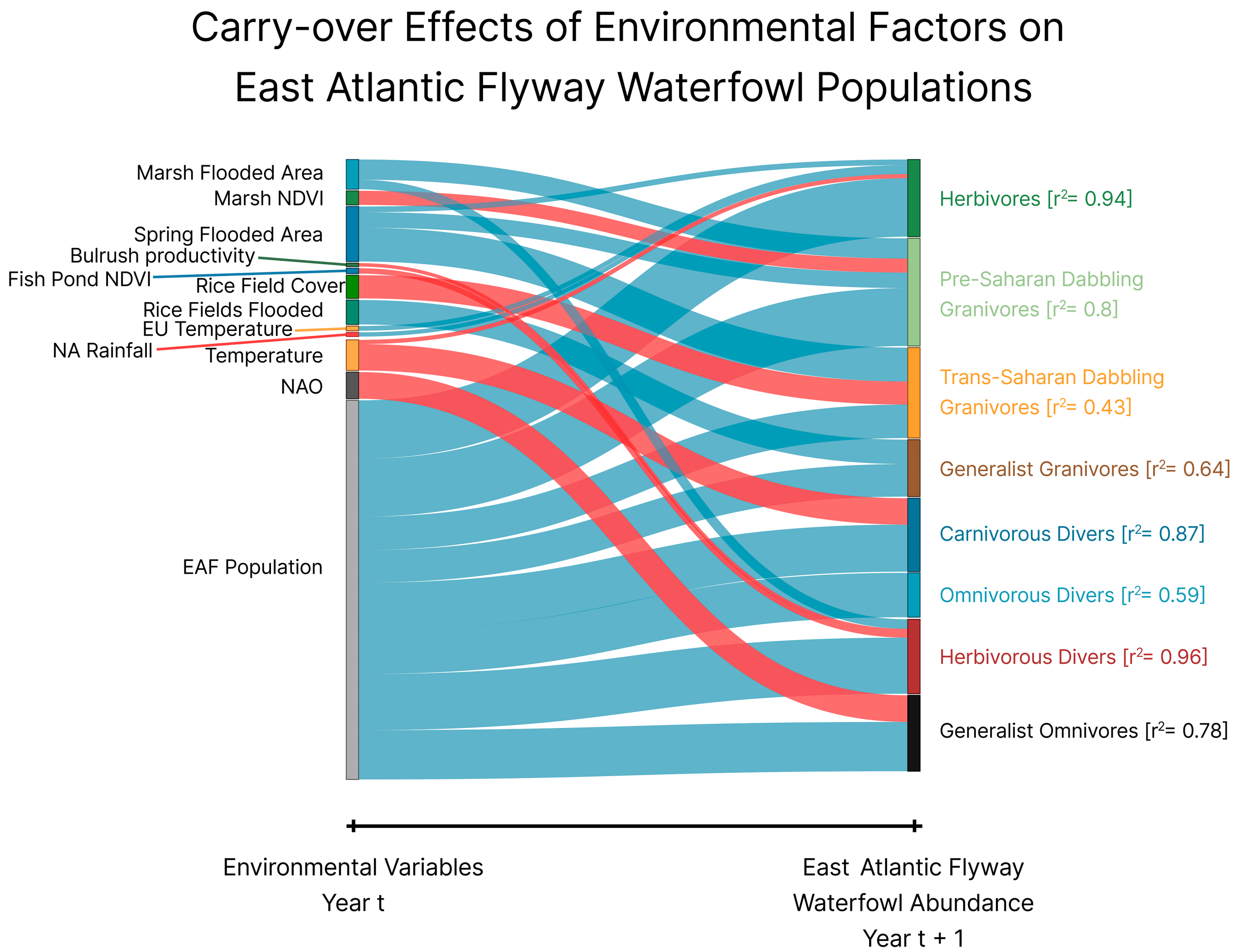


FIGURE 6 | Flow diagram depicting SEM significant standardised estimates of carry-over effects of wintering conditions in the Guadalquivir Marshes on waterfowl abundance in the following year, split by functional groups. Red links denote negative effects, whereas blue links depict positive ones. Link width is represented relative to the size of the effect. Conditional r^2 values of SEM for each functional group are indicated in brackets.

omnivores EAF populations were also negatively affected by NAO (Std. Est. = −0.40), whereas generalist granivores were positively affected by rice flooded area (Std. Est. = 0.37).

Diving waterfowl also showed environmental correlates. Carnivorous divers EAF populations in $t+1$ were negatively affected by mean temperature (Std. Est. = −0.40). Herbivorous divers were negatively affected by bulrush productivity (Std. Est. = −0.05) and fish pond NDVI (Std. Est. = −0.08), whereas marsh flooded area had a positive effect on the EAF populations on t + 1 (Std. Est. = 0.14). Moreover, omnivorous divers were only affected by EAF population size on t (Std. Est. = 0.67).

4 | Discussion

The Guadalquivir marshes represent the most important wetland in Western Europe and a major hub for migratory waterbirds at the crossroads of Europe and Africa. However, the wintering waterfowl community has undergone significant changes in both abundance and composition over the last 40 years. These changes were correlated to both, local and global factors. Changes in the environmental conditions at the GM were also correlated with changes in waterfowl populations across the East Atlantic Flyway, supporting the idea that changes in single wetlands of key importance can have carry-over effects on the entire biogeographical population of certain species.

4.1 | The Wintering Waterfowl of the Guadalquivir Marshes

Since 1984, the study area has shifted from a community of wintering waterfowl composed mainly by herbivores and pre-Saharan dabbling granivores to the current one dominated by Trans-Saharan dabbling granivores. Quantitative changes also occurred. Although Rendón et al. (2008) already detected long-term declines in four Anatidae species, we found that 10 out of the 15 species studied (represented by herbivores, pre-Saharan dabbling granivores, generalist granivores and carnivorous divers) experienced long-term negative trends, which resulted in a general decline in waterfowl wintering numbers in the study area. Moreover, six out of the 10 species experiencing negative trends (*A. anser*, *A. crecca*, *A. ferina*, *F. atra*, *M. penelope* and *M. strepera*) used to meet Ramsar Convention's 1% criterion of international importance, regularly gathering > 1% of the Western Palearctic population of such species in the GM, but are now under such threshold or at risk of not reaching it (Figure S1).

Wintering waterfowl abundances in the GM were related to both, local and global factors, although the sign and magnitude of these effects varied among functional groups according to their habitat and diet preferences. Wintering waterfowl in the GM were largely affected by the conditions of the natural marshes (e.g., flooded area, productivity, flooding date, etc.). Omnivorous divers were an exception, as their winter abundance in the GM was only explained by the management of anthropic wetlands (fish ponds and rice fields) and climatic oscillators (NAO).

Marsh flooded area stood out as the main factor explaining interannual changes in herbivore, pre- and trans-Saharan dabbling granivore waterfowl. Spring-flooded area had lagged, positive effects, on herbivores, which may be explained by the associated high productivity of helophytes and macrophytes that constitute their main winter food source. Marsh NDVI negatively impacted the winter abundance of pre-Saharan, trans-Saharan dabbling granivores and generalist omnivores. We can only but speculate about the reason behind this finding: species in these functional groups (*A. platyrhynchos*, *A. crecca* and *A. acuta*) are known to forage on agricultural lands (Bellrose and Kortright 1976; Delnicki and Reinecke 1986; Parejo et al. 2019), and higher NDVI values of non-flooded marsh areas could mean that part of the seedbank has already sprouted, making it unavailable for granivores as a food source. However, the causal mechanism by which NDVI values in non-flooded areas affect waterfowl abundances remains unsolved. Thus, a spurious result cannot be disregarded here either. Further research should aim to disentangle the nature of these relationships.

Carnivorous and herbivorous divers were positively affected by bulrush productivity, whereas generalist granivores experienced a negative effect. There are several potential explanations to this. Waterbirds have a good knowledge of their resource landscape at the migratory flyway scale, following an ideal free distribution in its wintering sites across NW Europe (Quaintenne et al. 2011). For instance, the positive effect on carnivorous divers could be related to a positive impact of an increase in invertebrate abundance through plant productivity, as found by Silva-Monteiro et al. (2022) for the density of breeding black-tailed godwits (*Limosa limosa*). Red-crested pochards (*N. rufina*) are known to preferentially winter in wetlands with abundant submersed macrophytes and extensive fringe vegetation (Madge and Burn 1988; Salvador, Amat, and Özgencil 2022). A preference for this habitat could be thus explaining the positive effects found, as bulrush stands represent the only emergent vegetation present in winter within the marsh open waters. However, the causal mechanisms by which wetland productivity drive changes in waterfowl assemblages and abundance remains unclear.

Delayed dates of marsh flooding were linked to lower winter numbers of herbivores, pre-Saharan dabbling granivores and carnivorous divers. Bulrush rhizomes together with helophyte seeds are stored in the dry clay substrate of the natural marshes. Early autumn rains soften this hardened soil, allowing waterbirds to access this resource, otherwise inaccessible for them (Amat, García-Criado, and García-Ciudad 1991). Early dates of flooding also ensure that herbivore waterfowl will encounter sufficiently grown submerged macrophytes at their time of arrival at the study area. Some waterfowl can compensate for adverse conditions by using alternative habitats (Amat and Ferrer 1988; Kloskowski et al. 2009). However, shifts towards later flooding dates may result in phenological mismatches that would force early arriving birds to either adjust their migration timing to the changing conditions or move to different wetlands or habitats. Being that none of these explanations are incompatible, further research should aim to explore the phenological mismatches of waterbirds in relation to resource variation and availability.

Rice field cover had a negative effect on omnivorous divers and trans-Saharan dabbling granivores. Our results attributed the marked positive trend of trans-Saharan dabbling granivores in the GM to the joint reduction of precipitation in North African Ramsar sites and the increase in Europe's autumn temperature, arguably shifting the wintering quarters of *A. acuta* and *S. clypeata* towards more northern latitudes, such as the GM. Moreover, generalist omnivores were positively affected by autumn temperatures in North African Ramsar sites, and negatively by winter temperatures at the GM. Migratory behaviour has been often understood as a resource-tracking mechanism (Herrera 1980; Piersma, Verkuil, and Tulp 1994). Climate change may thus be especially relevant for waterfowl individuals currently on the edge of their distribution ranges (and thermal tolerance), producing shifts towards more northern wintering locations in the northern hemisphere as new potential niches are created (Jiguet et al. 2010; Lehikoinen et al. 2013; Pavón-Jordán et al. 2018).

Almaraz and Amat (2004) analysed in detail the effect of climatic oscillators such as the NAO and ENSO on the expansion dynamics of *O. leucocephala* in Spain and found complex, lagged effects of both variables throughout the annual cycle. Although our study only encompasses part of the annual cycle, we found a positive effect of NAO on winter abundance of these diving omnivores in the study area. For instance, low precipitation in Spain during high NAO winters may have made permanent wetlands (such as those found in GM's fish ponds) an attractive, predictable waterbody that would attract birds otherwise dispersed throughout the Iberian Peninsula and North Africa; this would also explain the positive effect that the creation of the fish farms had on winter abundance of white-headed ducks in the GM as well as on the maintenance of its population at regional scale.

Overall, local abundances of waterfowl were uncoupled to the biogeographical trends experienced in the EAF but were correlated to a wide range of local and global environmental factors. Supporting that local and/or regional trends of migratory animals must be studied in the context of local and global factors.

4.2 | Correlates at the Flyway Scale

Population size on a given year was the best predictor of population size of all waterfowl functional groups on the following year. However, conditions experienced by wintering waterfowl at the GM also had significant effects on the EAF populations of 10 of the 15 species considered.

Marsh flooded area showed positive effects for pre-Saharan dabbling granivores and herbivorous divers, whereas spring-flooded area had a positive effect on herbivores and dabbling granivores (both pre- and trans-Saharan). These positive effects may be linked to the high primary production levels associated with wet years that may provide abundant and diverse food for wintering waterfowl feeding on plants and seeds.

Bulrush productivity showed negative effects on diving herbivores, likely due to a reduced submersed macrophyte abundance in areas with dense bulrush and floating vegetation (Duarte et al. 1990), what may impact herbivorous diver's diet. However, marsh hydroperiod may also play a role, as shorter hydroperiods benefit helophyte growth in detriment of macrophyte development. Regarding this matter, Díaz-Delgado et al. (2016) analysed the hydroperiod change in the natural marshes of Doñana National Park, finding a widespread reduction of hydroperiod since 1974. Contrastingly, no such effect was found on herbivore abundance. Some herbivores (e.g., greylag goose) may thus compensate low bulrush availability by shifting to alternative food sources like crops (Amat 1986).

Mean temperature in the GM had negative effects on both herbivores and carnivorous divers. This could be due to thermal preferences of these groups, which may be already close to their thermal maxima in the southernmost parts of their winter distribution; as found for other waterbirds (Lehikoinen et al. 2013; Pavón-Jordán et al. 2018). The NAO also had negative effects on generalist omnivores EAF populations, which may be due to NAO-associated rainfall patterns, as higher NAO is often associated with droughts in southern Europe (Gallego, García, and Vaquero 2005).

Trans-Saharan dabbling granivores are rice consumers (Clark et al. 2020; Dubowy, Carboneras, and Kirwan 2020). Up to 99% of the wintering diet of *A. acuta* in western Spain may be composed of rice seeds (Navedo et al. 2015). However, our results showed that rice field cover had a negative effect in *A. acuta* and *S. clypeata* abundances in the GM, and on their EAF populations in the next year. The marked increase in Trans-Saharan dabbling granivore populations at the GM should not be thus interpreted as a consequence of agri-environmental schemes or the creation of a fish pond complex (as invoked by Márquez-Ferrando et al. 2014 for *Limosa limosa*), but in a wider context where the reduction of autumn rainfall in North African Ramsar sites, and the increase in autumn temperature in the European ones, has shifted wintering sites to northern locations such as the GM (Figure 7), where the positive effects of both, marsh and spring-flooded areas, suggest that natural areas are preferential foraging sites against rice fields, which may be used in the absence of flooded natural marshes.

Fish pond NDVI values had negative effects on herbivorous divers. These waterbodies consist of large ponds of open waters, with a low abundance of submersed macrophytes (Rodríguez-Pérez and Green 2006), and where high NDVI values are driven mainly by primary production (i.e., phytoplankton). High phytoplankton productivity may be modulated by nutrient availability, and zooplankton, on which some herbivorous divers (such as *A. ferina*), may facultatively feed when the availability of macrophytes in the natural marshes is low (Cramp and Simmons 1977; Mouronval et al. 2007). However, future research should explore the nature of these relationships between primary production, zooplankton and waterfowl abundance.

Overall, natural marsh conditions (i.e., flooding or productivity) in the GM affected the EAF populations of 10 out of the 15 species

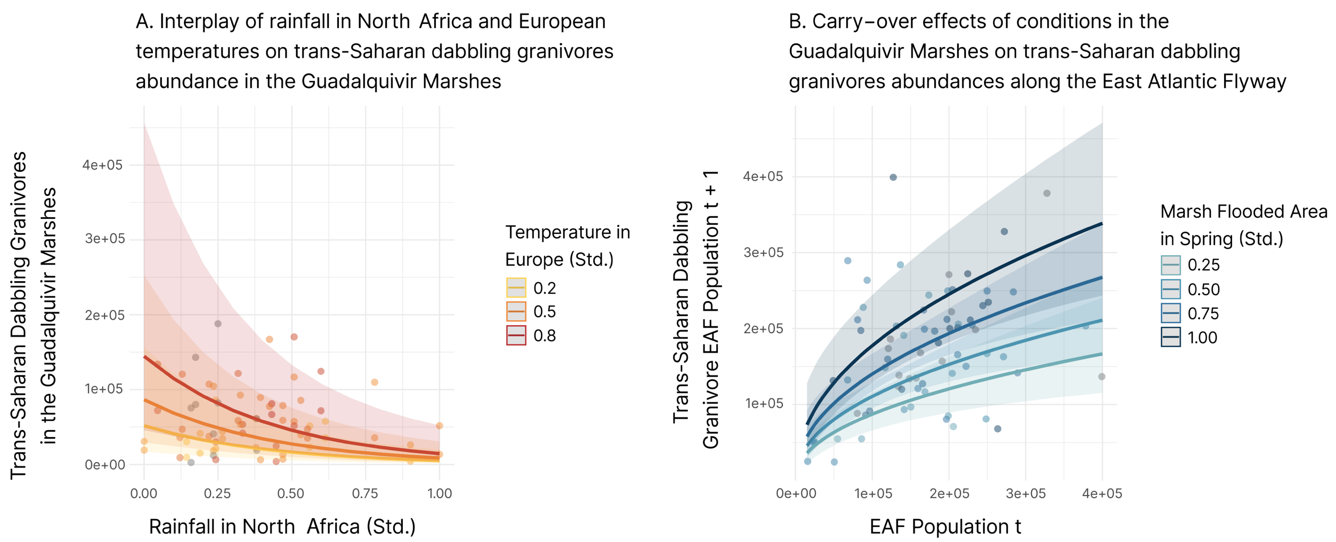


FIGURE 7 | Left: SEM predicted effects of rainfall in North African Ramsar sites and autumn temperature in European Ramsar sites on trans-Saharan dabbling granivore abundance in the Guadalquivir marshes. Right: SEM predicted effects of the interplay between the East Atlantic flyway population size in year *t* and maximum flooded area of the Doñana marshes in spring on trans-Saharan dabbling granivore abundance along the East Atlantic flyway in year $t+1$. Shaded areas represent 95% standard error.

studied. Regarding man-made wetlands, rice field flooded area was the only variable with a positive effect on generalist granivores. These results highlight the key role of the natural marshes of the Guadalquivir River for waterfowl conservation in the Western Palearctic, where the ecosystem services provided to waterfowl are not replaced by the management of human-made wetlands, such as rice fields, fish ponds or salt pans. These results align with those found by Sebastián-González and Green (2016), where bird diversity was higher in natural and restored wetlands as opposed to human-made ones and suggesting that resources for wetland conservation are usually better invested in restoration rather than in the creation of wetlands. However, some precaution should be taken here, as we only explored the effect of agri-environmental schemes on waterfowl and during a specific period of their life cycle (winter). Further research should aim to explore the effects of agri-environmental schemes over the whole waterbird community throughout the complete annual cycle.

Our work does not come without limitations: as is often the case, the nature of our findings is correlational, forming the basis upon which we infer causal relationships. Changes in the study area may correlate with those in other wetlands. However, the Guadalquivir marshes are approximately 2.3 and 3.5 times larger than the second and third most important wetlands for waterbirds in Iberia and North Africa, which harbour a proportionally lower number of waterbirds (Martí and del Moral 2002) and are artificially managed for rice cultivation, operating independently from GM. The scale and abundance of wintering waterfowl in the GM are thus of such magnitude that arguably no other wetland in Western Europe and North Africa could adequately sustain their populations. The deterioration of these critical wetlands may lead to lower bird survival and fitness. Which, in turn, may have carry-over effects on biogeographical populations of migratory waterbirds, as illustrated in Zwarts et al. (2009) for several waterbird species wintering in Sahelian Africa.

In the current context of widespread wetland transformation, it is crucial to both protect and manage wetlands to preserve their ecological processes. This work strides to provide land managers with a framework of wetland management for wintering waterfowl. We thus emphasise that wetland management and restoration should aim to create mosaics of dynamic natural habitats with different hydrological regimes (e.g., flooding date, flooding extent and flooding duration) and productivities (e.g., phytoplankton, helophytes and submersed macrophytes), which would ensure the maintenance of adequate wintering habitats for the waterfowl community.

5 | Conclusion

Over the last 40 years, the wintering waterfowl assemblage in the Guadalquivir marshes has undergone significant changes because of local and global factors. The abundance of wintering waterfowl in the GM was primarily affected by conditions encountered by birds within the study area and during migration. These conditions had significant effects on continental populations along the East Atlantic Flyway in the following year. By using the Guadalquivir marshes as a case study, this work highlights: (i) that changes in the flooding dynamics of the Guadalquivir marshes are impacting the diversity and composition of its waterfowl community, (ii) the importance of considering global factors and flyway population data when interpreting trends of migratory animals, and (iii) that changes in a single but critical wintering site can have measurable effects on species' biogeographical populations. Urgent measures are thus needed to halt the deterioration of the GM and safeguard the hundreds of thousands of waterbirds using this wetland every year.

Author Contributions

Miguel de Felipe: conceptualization, data curation, formal analysis, methodology, writing – original draft, writing – review and editing. **Juan A. Amat:** conceptualization, writing – original draft, writing – review and editing. **José Luis Arroyo:** data curation, investigation, writing – review and editing. **Rubén Rodríguez:** data curation, investigation, writing – review and editing. **Carmen Díaz-Paniagua:** conceptualization, funding acquisition, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13960897. Historical and current flooding data for the Doñana National Park marshes can be viewed using EarthEngine at https://migueldefelipe.users.earthengine.app/view/historical-marsh-monitoring. Remote sensing data is available from the U.S. Geological Survey at https://doi.org/10.5066/P9IAXOVV (Landsat 5), https://doi.org/10.5066/P9C7I13B (Landsat 7), and https://doi.org/10.5066/P9OGBGM6 (Landsat 8) can be viewed using EarthEngine at https://migueldefelipe.users.earthengine.app/view/historical-marsh-monitoring. Precipitation and temperature data are available from EU Copernicus at https://doi.org/10.24381/cds.f17050d7 (ERA5). Annual numbers of waterfowl in the Western Palearctic from Wetlands International's International Winter Census (IWC) are available in Zenodo at and https://doi.org/10.5281/zenodo.13960897 and can be requested from IWC at https://iwc.wetlands.org/index.php/aewatrends8.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.