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Vertebrate scavenger assemblages and their functioning differ between artificial and natural wetlands: Implications for ecosystem management

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ABSTRACT

Natural wetlands perform essential ecological functions, but their area has dramatically decreased. Partly to counteract this loss, artificial wetlands have been created. While studies comparing animal communities between artificial and natural wetlands abound, research on their comparative ecological functions is scarce. In particular, vertebrate scavengers in aquatic ecosystems have been little studied despite their critical role in nutrient cycling. This study compared vertebrate scavenger assemblages and their consumption patterns in natural and artificial wetlands in Doñana, Spain, to evaluate the effects of wetland management (natural vs. artificial hydrology) across different seasons. We placed 120 carcasses (carp and chicken) in natural and artificial wetlands. We recorded 22 vertebrate scavenger species efficiently consuming 100 % of carrion in an average of less than two days, highlighting their role in nutrient recycling. Carrion of aquatic-origin was consumed faster and by a greater variety of species than that of terrestrial-origin, facilitating the transport of essential nutrients from water to land. Artificial wetlands exhibited higher efficiency in carrion removal (twice as fast as natural wetlands). However, they hosted less diverse assemblages, dominated by opportunistic and non-native species. This suggests that artificial wetlands are not replacing natural wetlands in terms of biodiversity, despite sustaining water levels and functions. Importantly, 'kidnapping' water for irrigation reduces the ability of natural wetlands to maintain ecological functions provided by scavengers. Urgent regulation of water abstraction from aquifers, especially for crop irrigation, is necessary to maintain minimum groundwater levels, preserving the functionality and ecological processes of this critical wetland complex.

1. Introduction

Wetlands are critical for the functioning of Earth's ecosystems by performing key ecological functions such as carbon sequestration, nutrient fixation, water purification and biodiversity maintenance (Mitsch and Gosselink, 2015; Zedler and Kercher, 2005), while also supporting many threatened species (Collen et al., 2014). They also play a major role in human well-being, providing services such as food and fuel, flood prevention, and by supporting many cultural and economic activities (Turner et al., 2008). However, more than half of Europe's wetlands have been lost in the last three centuries (Fluet-Chouinard et al., 2023), mainly due to drainage and transformation for agriculture (Zedler and Kercher, 2005). In the Mediterranean region, approximately 50 % of the natural wetland area has been reduced during the 20th century, and the remaining wetlands continue to suffer further drainage and degradation, which reduces their capacity to provide ecosystem services (Perennou et al., 2020). In addition, most of the remaining natural wetlands have suffered alterations in their hydroperiod,

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diminishing both the extent and permanence of the water surface due to groundwater abstraction and declining precipitation (Díaz-Delgado et al., 2016; Green et al., 2024), which is expected to increase with climate change (Les Landes et al., 2014).

The loss of wetland habitats is to some extent compensated by the creation of artificial wetlands, currently representing 25 % of the surface area of Mediterranean wetlands (Perennou et al., 2012). This percentage is even higher in Spain, where approximately 75 % of the total wetland area consists of artificial wetlands (Perennou et al., 2012). Natural and artificial wetlands typically have radically different hydrodynamics. In the Mediterranean and other semi-arid regions, water levels in natural wetlands are highly dynamic, with many wetlands that only flood for part of the year, and only in some years. In contrast, artificial wetlands typically have relatively stable and predictable water levels owing to management for agriculture, aquaculture, recreation or conservation (Bustamante et al., 2016; Davidson and Finlayson, 2018). In natural wetlands, water levels drop quickly during dry periods, concentrating biomass of fish and other animals and promoting die-offs (e.g., DuBose et al., 2019) generating a large amount of dead biomass (i.e., carrion) that can trigger cascading effects on the ecosystem (Weber and Brown, 2016). Nevertheless, the extent to which these artificial wetlands can effectively substitute natural counterparts and fulfil their ecological roles remains uncertain.

Numerous studies have been conducted to assess the ability of artificial wetlands to replace natural ones, with a focus on species diversity and composition, particularly of waterbirds, amphibians, fish and macroinvertebrates (Sievers et al., 2018). Artificial wetlands have been shown to also confer substantial benefits to biodiversity (e.g., as stopover, breeding or foraging sites), especially when complemented with natural wetlands (Kloskowski et al., 2009; Li et al., 2013). However, the success of these wetlands is context-dependent (Meli et al., 2014), and relies on factors such as wetland type (Li et al., 2013), construction methods (Wiegleb et al., 2017), physicochemical characteristics (Bellio et al., 2009), or hydroperiod (Coccia et al., 2024) among others. More importantly, studies comparing the ecological functions performed by the fauna in different types of wetlands are much scarcer. Almeida et al. (2020) reported lowers functional avian diversity in artificial wetlands created for a conservation purpose than in restored and natural wetlands, but artificial wetlands designed for fish production exhibited a higher functional richness during winter. However, it is not yet known how the type of wetland can impact ecological functions such as seed dispersal, predation or scavenging.

The vertebrate scavenger guild in wetlands has received comparatively less attention than in terrestrial ecosystems (Orihuela-Torres et al., 2024). Both obligate and facultative scavengers play a critical role in ecosystems by efficiently recycling nutrients through carrion consumption. They consume substantial amounts of carrion over a short time period (Moleón et al., 2015), thereby stabilizing the food web (Wilson and Wolkovich, 2011), preventing the spread of pathogens and disease (Markandya et al., 2008) and limiting greenhouse gas emissions (Morales-Reyes et al., 2015). Furthermore, wetlands are highly productive ecosystems that attract a high diversity of species in a relatively small area, leading to the production of substantial quantities of carrion (Szlauer-Łukaszewska et al., 2024; Weber and Brown, 2016). By consuming carrion in these ecosystems, scavengers prevent water eutrophication (Santori et al., 2020) and transport nutrients between and within aquatic and terrestrial systems (Gabel et al., 2019; Orihuela-Torres et al., 2022). Nevertheless, general scavenging dynamics are influenced by several factors such as seasonality or carcass type. Wetlands are usually highly seasonal ecosystems fluctuating throughout the year, and seasonality also drives carrion consumption patterns (Vandersteen et al., 2023) and alters scavenger assemblages (Orihuela-Torres et al., 2022). However, most studies conducted in wetlands do not take seasonality into account (Orihuela-Torres et al., 2024). Moreover, another crucial factor in scavenging dynamics is the carcass type (i.e., species or guild) (Olson et al., 2016) and its origin (i.e., aquatic or terrestrial), which may lead to a shift between different ecosystems in the scavenger assemblages (Redondo-Gómez et al., 2022).

Doñana is one of the most important wetland complexes in the Western Palearctic (Green et al., 2018). It is formed by several natural wetlands whose dynamics are highly dependent on annual variations in precipitation directly (direct rainfall) or indirectly (groundwater recharge), leading to large water level fluctuations and frequent desiccation during part of the year (natural hydrology). There are also some artificial wetlands located in former seasonal marsh areas, that were created using dikes to increase water capacity. These ponds were built for aquaculture or conservation purposes and exhibit an artificial hydrology with active management, which differs significantly from the hydrology of natural wetlands (Almeida et al., 2020). They maintain relatively stable water levels throughout the year, controlled by sluice gates and by pumping water (Walton et al., 2015). However, the dynamics of natural wetlands are being heavily impacted. In recent years, Doñana, as well as most of the Mediterranean region, has been facing a particularly severe drought (Green et al., 2024; Rogers et al., 2022). Moreover, groundwater abstraction for greenhouse farming and other human uses has greatly increased in the Doñana catchment area in recent decades (Paredes et al., 2021), which is negatively affecting natural wetlands, reducing their surface area and hydroperiod, and even leading to complete desiccation of many temporary and permanent ponds (de Felipe et al., 2023; Dimitriou et al., 2017), and is even altering the terrestrial vegetation surrounding the wetlands (Green et al., 2024).

The main objective of our study was to compare vertebrate scavenger assemblages and their functioning between natural and artificial wetlands in Doñana, to assess the impact of wetland management (natural vs. artificial hydrology), in different seasons. Furthermore, we compared the scavenging dynamics among different types of carcasses, representing aquatic subsidies (i.e., fish) and terrestrial subsidies (i.e., chicken). Our general hypothesis is that wetland management will influence the scavenger species composition and carrion consumption patterns. As natural wetlands were shallow and ephemeral during the study period, we predicted that artificial wetlands would attract larger populations and greater numbers of scavenging species, especially birds, due to their permanent water surface (Walton et al., 2015). Consequently, we predicted that carcasses would persist in the ecosystem for longer time periods in natural wetlands. Moreover, we expected that seasonality would influence the scavenger assemblage, particularly for avian species, given their migratory nature which can impact carrion consumption patterns (Vandersteen et al., 2023; Parmenter and Macmahon, 2009). Additionally, we predicted that aquatic subsidies would be consumed more rapidly than terrestrial ones since scavengers frequent shorelines in search of food, where these types of carcasses appear (Schlacher et al., 2020). Finally, we discuss the implications of our study for integrative water management of natural and artificial wetlands.

2. Methods

2.1. Study area

Our study was conducted in Doñana Natural Space (108,429 ha), which includes a National and the Natural Park, located in the Guadalquivir estuary, south-western Spain (Fig. 1). It was declared a Biosphere Reserve in 1980, an Internationally Important Wetland under the Ramsar Convention in 1982, and a UNESCO World Heritage Site in 1984. Doñana is made up of a heterogeneous mosaic of wetlands comprising seasonal marshes located in a floodplain fed by surface flow and direct rainfall, and a dune system that holds >3000 temporary ponds fed by groundwater (Díaz-Paniagua et al., 2010; de Felipe et al., 2023). Doñana is a key location for bird migration, is a critical site for waterbirds (Rendón et al., 2008), and is one of the last major natural coastal ecosystems in Europe. It has a Mediterranean climate with Atlantic influence. The mean annual temperature is 17 °C with hot, dry

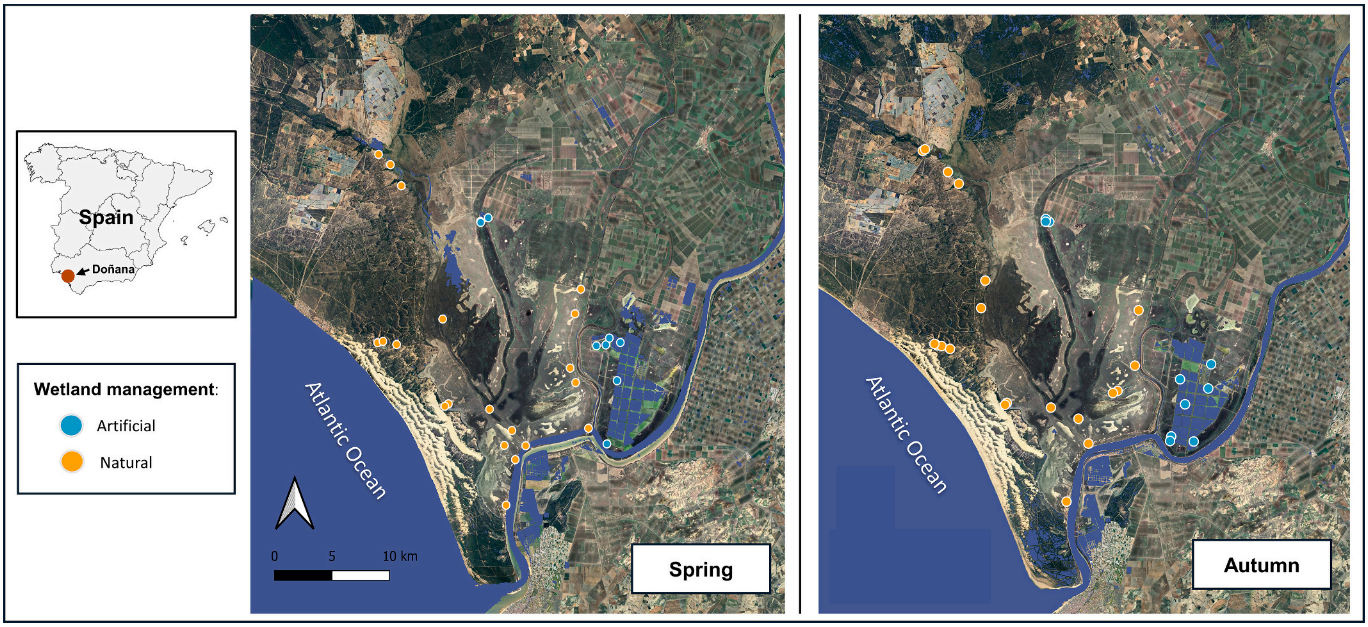

Fig. 1. Map of the study area in Doñana (south-western Spain) showing the extent of standing surface water (coloured dark blue) on two days during the field work (4/11/2023 Spring and 10/8/2021 Autumn). The locations of 60 paired (fish and chicken) carcasses in different seasons (spring and autumn; 30 paired carcasses per season) to detect the vertebrate scavenger assemblage in artificial (blue points; 20 paired carcasses) and natural (orange points; 40 paired carcasses) wetlands are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

summers (mean 23.5 °C) and short, mild winters (mean 10.9 °C). Rainfall is concentrated between October–April, with dramatic inter-annual variation (mean annual rainfall: 550 mm; range 170–1027 mm). However, while our study was carried out in autumn 2021 and spring 2023, rainfall and the flooding extent of natural wetlands were well below average (Camacho et al., 2022; Green et al., 2024).

Doñana holds a rich vertebrate community. The potential vertebrate scavenger species include top carnivores, such as Iberian lynx (*Lynx pardinus*), and mesocarnivores like the red fox (*Vulpes vulpes*), Egyptian mongoose (*Herpestes ichneumon*), common genet (*Genetta genetta*), Eurasian badger (*Meles meles*) or Eurasian otter (*Lutra lutra*) (Palomares et al., 2011). It also hosts an abundant wild boar (*Sus scrofa*) population. These mammals coexist with a diversity of raptors such as the Spanish eagle (*Aquila adalberti*), black kite (*Milvus migrans*), red kite (*Milvus milvus*), western marsh harrier (*Circus aeruginosus*), and obligate scavengers, i.e., vultures, namely the Eurasian griffon (*Gyps fulvus*) and cinereous vulture (*Aegypius monachus*) (Ferrer and Calderón, 1990; Sergio et al., 2005). Among waterbirds, key scavengers are gulls.

2.2. Field methods

To evaluate the effect of wetland management on scavenging dynamics, we classified Doñana wetlands according to their hydrology. We considered as ‘natural wetlands’ those that are fed by surface water flow and direct rainfall or fed by aquifers, thus maintaining a natural hydrology with large water level fluctuations, usually drying out for part of the year. This group also includes *caños* (historical tidal or stream channels). Salinity varies from freshwater to saline. During our study, both autumn 2021 and spring 2023 were extremely dry periods due to the low precipitation and the impact of groundwater abstraction, so that surface water in natural wetlands was scarce and ephemeral, and was even absent in some areas during fieldwork (Fig. A.1) (Green et al., 2024).

‘Artificial wetlands’ were those created by diking to increase water retention, with an artificial hydrology and relatively stable water levels throughout the year. To maintain stable water levels all year round, active water management is implemented through pumping and a system of sluice gates that supply these artificial wetlands. This hydrology is very different from that of natural wetlands, which exhibit much more pronounced water level fluctuations. These artificial wetlands included saline fish ponds maintained by circulating water from the Guadalquivir estuary (Walton et al., 2015), and freshwater ponds flooded with groundwater pumped from the aquifer (Fig. A.2).

To identify the vertebrate scavenger assemblage present in Doñana wetlands, we used different carcass types from terrestrial and aquatic origin in different wetlands and seasons. We selected wetlands based on water availability during the fieldwork period (i.e., we excluded those that were totally dry). We placed 30 paired carcasses in autumn 2021 (October–November) and 30 in spring 2023 (April–May), i.e., 120 carcasses in total. Each carcass pair comprised a) an aquatic subsidy, the common carp (*Cyprinus carpio*; 563.2 ± 294.5 g) placed on the water shoreline to mimic natural mortality, and b) a terrestrial subsidy, an organically raised chicken (*Gallus gallus*; 1814.2 ± 673.8 g), placed 50–100 m away from the common carp and the shoreline in terrestrial habitat. We used common carp as aquatic-origin carrion due to its prevalence in the Doñana wetlands (e.g. Walton et al., 2015). Similarly, chickens were selected as terrestrial-origin carrion because they are among the most commonly used in scavenging studies worldwide (e.g. Butler-Valverde et al., 2022; Gabel et al., 2019). The chickens were always located in shrubby areas with good visibility, to ensure that the visual detectability of both carcass types was similar. Although the vegetation in the artificial wetlands was generally more homogeneous than in the natural ones, many plant species were shared among the two wetland types, and the structure of the vegetation was similar. The predominant vegetation surrounding both artificial and natural wetlands consisted of species typical of saltmarshes, such as *Arthrocnemum macrostachyum*, *Salsola vermiculata*, and *Suaeda vera*. Additionally, in some natural wetlands further west in Doñana, shrubs such as rosemary (*Salvia rosmarinus*), wild chamomile (*Helichrysum picardii*), heather (*Erica* spp.), narrow-leaved mock privet (*Phyllirea angustifolia*), mastic (*Pistacia lentiscus*) and gorse (*Ulex minor*) predominate (Fig. A.3). The carcass pairs were placed simultaneously and separated by at least 300 m; usually more than one km apart. Forty paired carcasses were placed in natural wetlands (20 pairs per season) and 20 pairs in artificial wetlands (10 pairs per season). The difference in sample sizes is due to the much larger maximum surface area occupied by natural wetlands.

Carcasses were monitored using motion-triggered remote cameras (Browning Strike Force HD pro). At each carcass, we placed two cameras with different schedules, both activated by movement: 1) photo mode, which took two photos every 20 s, and, 2) video mode, to confirm carrion consumption by the detected species, which took a 10-s video every 30 s. Cameras were placed on stakes 60–100 cm high and 1.5–2 m away from the carcass. Carcasses were checked every 2–3 days, and cameras were left until the carcass was completely consumed (except for the skeleton and skin or feathers) or removed by a scavenger.

The necessary permits for this study were obtained from the administration (Junta de Andalucía, ref. number: 2021/08).

2.3. Scavenging metrics

We calculated the following variables to assess the scavenging dynamics: I) *species richness*, i.e., the number of vertebrate species recorded feeding on each carcass. We calculated this variable for birds, mammals, and in total; II) *carcasses scavenged first*, i.e., percentage of carcasses first scavenged by birds or by mammals; III) *scavenged carcasses*, i.e., percentage of carcasses where birds and mammals were recorded consuming; IV) *first scavenging event*, i.e., time elapsed from carcass exposure until the first scavenger started to consume the carcass; V) *consumption time*, i.e., time it took for scavengers to completely consume the carcass; VI) *vertebrate scavenger assemblage composition*, i.e., species identities and their relative abundances. Abundance was estimated as the maximum number of unequivocally different individuals (identified by having different age, sex or body features) recorded at a carcass.

2.4. Data analysis

We fitted Generalized Linear Mixed Models (GLMMs) to test the effect of *wetland management*, *carcass type* and *season* on the scavenging efficiency of the vertebrate scavenger assemblage. We used *first scavenging event* and *consumption time* as response variables with Gamma distribution error. *Wetland management* (natural vs. artificial), *carcass type* (aquatic vs. terrestrial subsidy) and *season* (spring vs. autumn) were used as factors, including the interactions between them. The ID of each paired carcass was included as a random factor to account for the relatedness of carcass pairs. We ran one model for each response variable. To fit the GLMMs, we used the *glmer* function in the *lme4* package (Bates et al., 2007). We explored all alternative models using the function dredge in the *MuMIn* package (Bartoń, 2023) and selected the model with the lowest AICc. When we had more than one candidate model (models with an ΔAICc <2), we calculated model-averaged coefficients using the *model.avg* function in the *MuMIn* package (Bartoń, 2023). To assess the contribution of the random factor in the models, we computed both the marginal (R^2m) and conditional R^2 (R^2c) for the best candidate model using the 'r.squaredGLMM' function from the *MuMIn* package (Bartoń, 2023). The analyses were performed in R 4.3.1 (R Core Team, 2021).

Finally, we compared the *vertebrate scavenger assemblage composition* between *wetland management*, *carcass type* and *season*, separately, using the permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a non-parametric test that analyzes differences in the matrix of relative abundances of the different species in samples from different groups (Anderson, 2001). This analysis was performed using the *vegan* package (Oksanen et al., 2019) in R 4.3.1 (R Core Team, 2021).

3. Results

3.1. Overall scavenging dynamics

We recorded 22 vertebrate scavenger species (10 mammals, 12 birds; Fig. A.4 and A.5) feeding on carrion (Table A.1). Scavengers were highly efficient, consuming 100 % of the carrion in a mean time (±SD) of 41.1 ± 50.9 h. Although more bird species were recorded, mammals fed on 92 (82.1 %) carcasses while birds fed on 41 (36.6 %) carcasses (Table A.1). We observed a temporal segregation in carrion consumption, with birds feeding exclusively during the day, while mammals primarily fed at night. The species that consumed by far the most carrion was the red fox, which fed at more than half of the carcasses ($n = 66$; 58.9 %), followed by the wild boar ($n = 11$; 9.8 %), the black kite ($n = 10$; 8.9 %), the yellow-legged gull (*Larus michahellis*; $n = 9$; 8 %) and the Egyptian mongoose ($n = 7$; 6.3 %). Furthermore, two non-native species were recorded consuming carcasses, the brown rat (*Rattus norvegicus*; n = 6; 5.4 %) and the feral dog (*Canis lupus familiaris*; n = 1; 0.9 %) (Table A.1).

3.2. Carrion consumption patterns

First scavenging event was three times shorter in artificial than in natural wetlands (15.5 vs. 44 h). Similarly, consumption of fish started much earlier than that of chickens (18.9 vs. 48.6 h) (Fig. 2). Such patterns were consistent between seasons (Table A.1). In the averaged model, only *wetland management* was significant ($p < 0.05$) whereas *carcass type* and the interaction between them were marginally significant ($p = 0.05$–0.1; Table A.2 and A.3). The fixed factors explained a significant part of the variance ($R^2m = 54.06$ %), while the contribution of the random variable to the best model was negligible ($R^2c = (R^2m)$ (Table A.3).

Consumption times were twice as fast in artificial wetlands than in natural wetlands (23.1 vs. 50.5 h), with fish being consumed much faster than chickens (26.9 vs. 54.6 h) (Fig. 2). As for the other response variables, we found no differences between *seasons* ($p > 0.05$; Table A.1). The averaged model included also *season*, the interaction between *wetland management* and *carcass type*, and the interaction between *season* and *wetland management*. *Wetland management* and *carcass type* had a significant effect, but *season* and their interaction with *wetland management* were not significant (Table A.2 and A.3). The fixed factors explained a significant part of the variance ($R^2m = 28.07$ %), while contribution of the random variable to the best model was lower (R^2c - $R^2m = 18.61$ %) (Table A.3).

3.3. Changes in scavenger species composition

We found differences in *vertebrate scavenger species composition* between *wetland management* (PERMANOVA, $F = 2.566$, $p = 0.032$), *carcass type* (PERMANOVA, $F = 10.845$, $p < 0.001$) and *season* (PERMANOVA, $F = 4.264$, $p = 0.004$) (Table A.4).

Regarding *wetland management*, we recorded a higher number of species consuming carrion in natural wetlands (ten mammals, eight birds) than in artificial wetlands (six mammals, six birds; Table A.2). Mammals were recorded in similar numbers in the two wetland types (artificial 86.8 % vs. natural 89.2 % of the carcasses), while birds were more frequent in artificial wetlands than in natural wetlands (36.8 % vs. 24.3 % of the carcasses respectively). Among mammals, the species group which differed the most with *wetland management* was rodents, especially the brown rat, which was relatively common in the artificial wetlands but absent in natural wetlands (15.8 % vs. 0 % of the carcasses), while the opposite occurred for mesocarnivores (Egyptian mongoose, common genet, Eurasian badger, Eurasian otter and feral dog) (artificial 5.3 % vs. natural 12.1 %) and wild boar (artificial 2.6 % vs. natural 13.5 % of the carcasses, Fig. 3; Table A.1). Regarding birds, gulls consumed much more carrion in artificial wetlands than in natural wetlands (20.8 % vs. 2.7 % of the carcasses), as did the western marsh harrier (10.5 % vs. 1.4 % of the carcasses) (Fig. 3; Table A.1).

The vertebrate scavenger assemblage differed significantly between *carcass types* (Tables A.1 and A.4). Fish were consumed by more species (eight mammals, nine birds) than chickens (seven mammals, eight birds). Mammals fed on almost all chicken carcasses (96.5 %) whilst birds played a less relevant role, scavenging on 13.8 % of the carcasses. However, birds played an important role for the recycling of fish carrion, feeding on almost half of the carcasses (44 %) whereas mammals

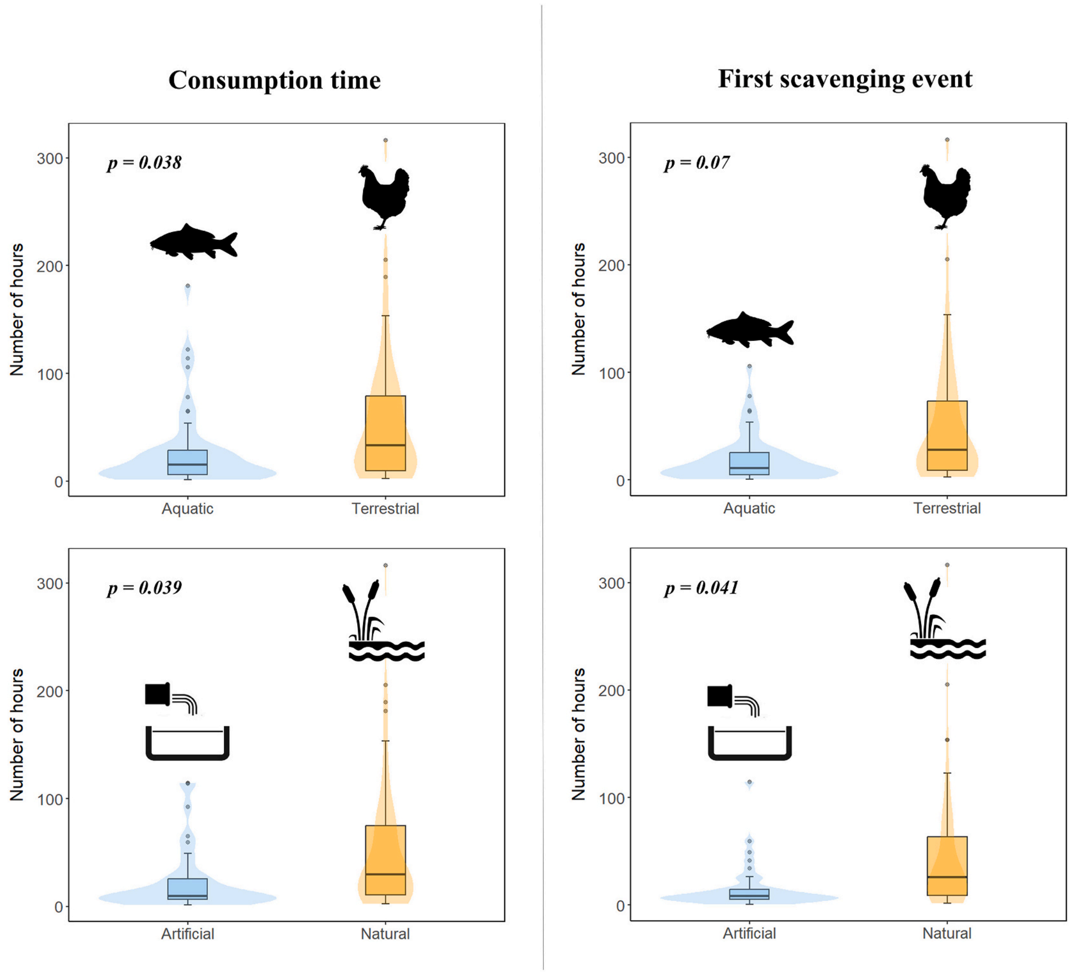

Fig. 2. (2-column fitting image). Consumption patterns of the vertebrate scavenger assemblage in Doñana wetlands. Figures are boxplots for the consumption pattern variables (*first scavenging event* and *consumption time*) that showed significant differences between *carcass types* (aquatic vs. terrestrial origin) and *wetland management* (artificial vs. natural). The standard deviation is shown as error bars, and the shadows show data distributions. We include the *p*-value (*p*) of the generalized lineal mixed models (GLMMs). See Table A.2 for details of analyses.

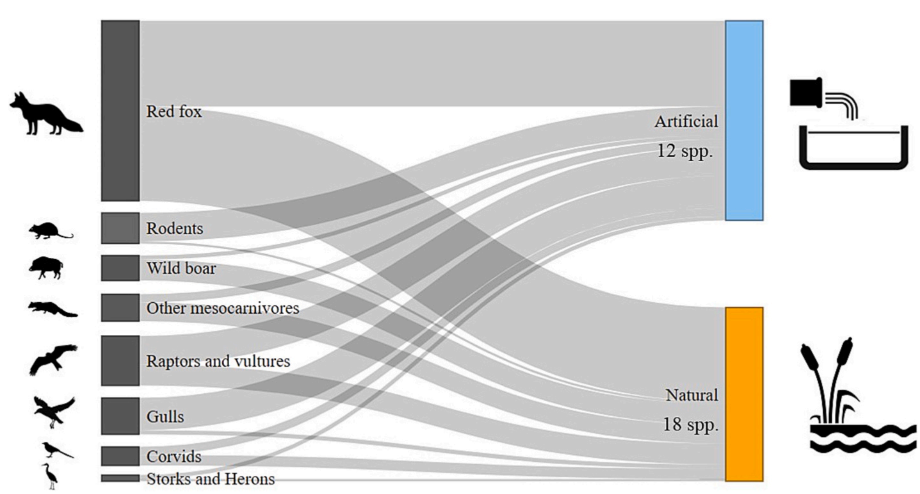

Fig. 3. (2-column fitting image). Interaction network showing the frequency of interactions between vertebrate scavengers and carrion in the different types of *wetland management* (natural and artificial) in Doñana. The width of left-hand bars (i.e. scavenger species/group bars) and linkages are proportional to the percentage of carcasses at which they were recorded feeding. The widths of the right-hand bars are proportional to the total number of consumption events by all scavengers. The figure shows red fox, rodents (brown rat, black rat, wood mouse), wild boar, other mesocarnivores (Egyptian mongoose, common genet, Eurasian badger, Eurasian otter and feral dog), raptors and vultures (western marsh harrier, black kite, red kite, common buzzard, Eurasian griffon and cinereous vulture), gulls (black-headed gull and yellow-legged gull), corvids (Eurasian magpie and common raven) and storks and herons (white stork and grey heron). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occurred less frequently (66.6 %) than on chicken carcasses. The red fox monopolized chicken carcasses, feeding on most of them (79.3 %), whereas it occurred less on fish carrion (37 %). However, other mesocarnivores such as the Egyptian mongoose, common genet, Eurasian badger, or Eurasian otter consumed more fish (12.9 %) than chicken carcasses (6.8 %). As for birds, raptors fed on twice as many fish carcasses as chickens (20.4 % vs. 10.2 %), especially the black kite (14.8 % fish vs. 3.4 % chicken). Gulls also fed much more and exclusively on fish carrion (22.3 % fish vs. 0 % chicken) (Fig. 4; Table A.1).

Season strongly influenced the *vertebrate scavenger assemblage composition* consuming carrion in Doñana (Table A.1 and A.4). In autumn, a higher number of species were recorded (nine mammals, seven birds) than in spring (four mammals, nine birds). Mammals fed at similar percentages of carcasses in the different *seasons* (≈ 82 %) while birds scavenged on slightly more carcasses in spring (31.6 % vs. 25.4 %). As for mammals, the red fox consumed much more carrion in spring than in autumn (70.2 % vs. 47.3 %), while for the other mesocarnivores the opposite occurred, being absent in spring (0 % vs. 20 %). For birds, the most pronounced differences were in the western marsh harrier (spring 0 % vs. autumn 9.1 % of carcasses), the black kite (spring 17.5 % vs. autumn 0 % of the carcasses) and the black-headed gull (*Chroicocephalus ridibundus*) (spring 5.3 % vs. autumn 0 % of the carcasses).

4. Discussion

Carrion decomposition and nutrient recirculation are processes modulated by a multitude of biotic and abiotic factors (Turner et al., 2017). Within these factors, a wide variety of human disturbances interact, influencing the fate of carrion (e.g., Gilby et al., 2023; Orihuela-Torres et al., 2023), and human influence is expected to become ubiquitous and increasingly determinant in scavenging dynamics (Bartel et al., 2024; Barton et al., 2023). Our study suggests that *wetland management* (i.e., modification of water surface and hydroperiod) alter scavenger assemblages and the carcass removal process. We found that scavenger assemblages in managed (i.e., artificial) wetlands were different and much more efficient at detecting and consuming carrion compared to natural wetlands. We also found differences in scavenging dynamics between types of carcasses. Aquatic-origin carcasses (i.e., fish) were consumed twice as quickly and by a different scavenger assemblage with a greater number of species, compared to terrestrial-origin carcasses (i.e., chickens). However, despite the seasonal variations in vertebrate scavenger assemblages, with more bird species in spring and more mammals in autumn, we did not find seasonal differences in overall consumption rates.

The vertebrate scavenger assemblage in this important wetland was extremely efficient, consuming 100 % of the carrion in a mean time of

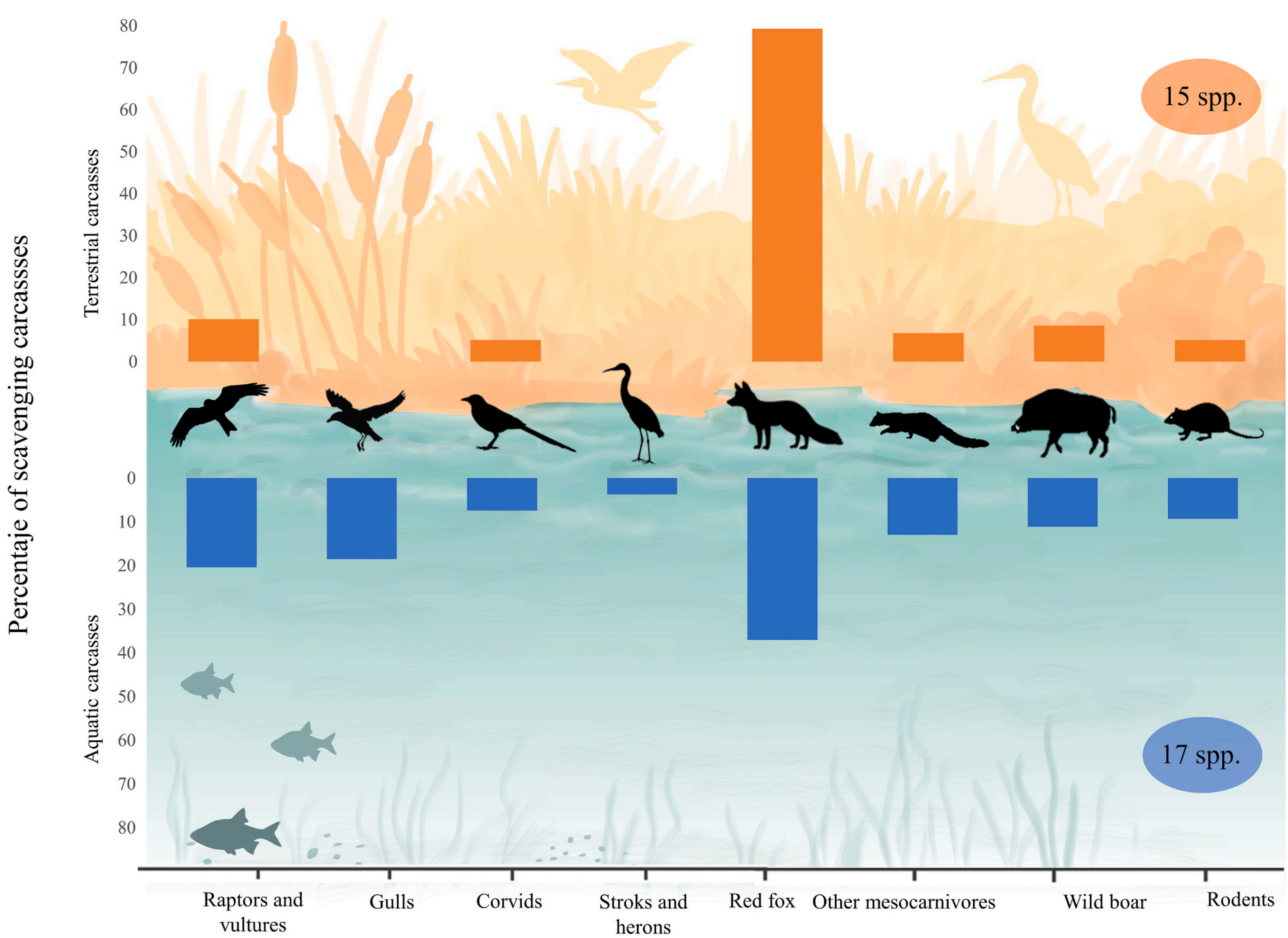

Fig. 4. (2-column fitting image). Vertebrate scavenger species recorded in Doñana wetlands consuming carrion of different *carcass types*; aquatic carcasses (carp; blue) and terrestrial carcasses (chickens; orange). The number of species that consumed each *carcass type* is also shown. The figure shows red fox, rodents (brown rat, black rat, wood mouse), wild boar, other mesocarnivores (Egyptian mongoose, common genet, Eurasian badger, Eurasian otter and feral dog), raptors and vultures (western marsh harrier, black kite, red kite, common buzzard, Eurasian griffon and cinereous vulture), gulls (black-headed gull and yellow-legged gull), corvids (Eurasian magpie and common raven) and storks and herons (white stork and grey heron). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

less than two days. Other studies conducted in wetlands reported that vertebrate scavengers consumed 73 % of fish carcasses in Spain (Orihuela-Torres et al., 2022) and 72.7 % in Canada (Etherington et al., 2023), or 85 % of chicken carcasses in USA (Gabel et al., 2019). This highlights the significant role played by vertebrate scavengers in Doñana, recycling a large amount of nutrients from carrion into higher trophic levels (Wilson and Wolkovich, 2011). Hiraldo et al. (1991) studied the vertebrate scavenger assemblage consuming greylag geese (*Anser anser*) carcasses in Doñana and recorded 11 bird species, of which only the Spanish eagle and lesser black-backed gull (*Larus fuscus*) were not recorded in our study. However, unlike our study, where ten mammal species appeared and consumed most of carcasses, Hiraldo et al. (1991) only reported two mammal species (red fox and wild boar), with birds consuming the majority of the carrion biomass. These differences may be due to the methodology used, as Hiraldo et al. (1991) studied carcass consumption though direct observations done during the day, when mammals are less active (Ferreiro-Arias et al., 2021). Also, the number of carcasses they used was smaller, and there have been some changes in the population sizes of mesocarnivores since then (Ferreras et al., 2011).

Scavenger assemblages and their dynamics differed greatly between natural and artificial wetlands. Birds such as gulls or marsh harriers, that associated with water surfaces, were recorded at one-third of the carcasses in artificial wetlands, yet were almost absent in natural wetlands, which had much smaller water surfaces and shorter hydroperiods. Contrary to the fluctuating water levels in natural wetlands, artificial wetlands are managed to maintain a stable water level throughout the year, making the presence of some resources (e.g. fishes) more predictable, thus facilitating foraging (Rendón et al., 2008). They also contain nesting sites for many species on islets and dikes, attracting a large number of Laridae and other birds. When natural wetlands are mostly dry, as happens regularly in the study area and is expected to happen more often with climate change, artificially maintaining some areas with water may preserve some of the animal communities and their functions in the ecosystem. However, the concentration of certain species into artificial wetlands may weaken the ecosystem services of adjacent natural systems if they are not well preserved.

In our study, scavengers found carrion three times faster in artificial wetlands than in natural ones, which may be due to higher abundances of birds, that are more efficient at locating carrion in open areas than mammals (Oliva-Vidal et al., 2022). Consequently, scavenger guilds had a greater efficiency in carrion removal in artificial wetlands (they did it in half the time). Regarding mammals, we found a higher diversity of mesocarnivore species in natural wetlands (6 spp. natural vs. 2 spp. artificial) likely due to greater habitat heterogeneity (e.g., different types of ponds, vegetation cover), although it is worth noting that we placed more carcasses in natural wetlands. The same happened with the wild boar, which was much more abundant in natural wetlands, as was the case in another Mediterranean wetland where this species only consumed carrion in areas with less human presence (Orihuela-Torres et al., 2023). This may be due to intensive hunting to control the species until a few years ago in Veta La Palma, one of our artificial study areas. Additionally, non-native species appeared exclusively in the artificial wetlands, and only one feral dog was recorded consuming carrion in the natural wetlands, but in a marsh adjacent to a National Park Visitor Centre. The same was recorded by Orihuela-Torres et al. (2023) in another Mediterranean wetland, where invasive species were four times more abundant in areas with human presence. This may alter not only scavenging dynamics (Newsome et al., 2024), but also the functioning of wetlands (Strayer, 2010).

Although *wetland management* seems to be a key factor in structuring scavenging dynamics, numerous internal factors are involved in this process. In Doñana, we can find a wide variety of artificial wetlands dedicated to conservation or fish farms, such as the ones where we conducted the study, as well as extensive rice fields and salt pans (Green et al., 2018). These different types of artificial wetlands will have varying characteristics such as vegetation structure, water surface area, salinity, etc., which will determine the associated biodiversity (Almeida et al., 2020; van Rees et al., 2021) and consequently, scavenging dynamics. It would be interesting to carry out future studies on scavenger assemblages and their functioning in the other artificial wetlands to better understand the scavenging dynamics in Doñana. Moreover, it would be of interest to compare how scavenging dynamics varies between natural and artificial wetlands when natural wetlands have good water levels.

It is also important to notice that the spatial distribution of the carcasses placed in artificial and natural wetlands in the landscape was not totally random, following the distribution of the different wetland types. Besides, the carcasses were placed at distances that can be reached by the same individual of some of the scavenger species within the same day. However, our results revealed significant differences in vertebrate scavenger assemblages between wetland types, emphasizing variations in scavenger use of artificial and natural wetlands and the impact of the wetland management.

Scavenger assemblages and their functioning also varied according to the *carcass type*. Fish were detected and consumed in half the time compared to chickens, and by different scavenger assemblages. Carrion of aquatic origin tends to be stranded on the shores, and these areas are frequented by scavengers in search of food (Schlacher et al., 2020). Furthermore, phylogenetic distance also plays an important role in carrion consumption, with species tending to avoid consuming carrion from phylogenetically closer species, probably to avoid disease transmission (Redondo-Gómez et al., 2022). This could be one reason why birds consumed three times more fish than chicken carrion. This efficient consumption of aquatic-origin carrion by terrestrial scavengers may have significant implications, at both the ecosystem and global scale. Due to the drastic declines in megafauna, as well as bird colonies and anadromous fish, the transport of key nutrients like phosphorus from water to land has been dramatically decreased, becoming a limiting factor in some ecosystems (Doughty et al., 2016). By consuming carrion of aquatic origin, vertebrate scavengers rapidly recycle and transport a large quantity of nutrients, including phosphorus, from water to land, playing a crucial role that may become even more relevant in the future (Barton et al., 2023). In North America, vertebrate scavengers fertilise riparian forests by transporting salmon carcasses and their excrement (Cederholm et al., 1999). Additionally, scavenger birds can transport nutrients not only to adjacent areas but also over large distances, connecting different ecosystems (Payne and Moore, 2006).

Similarly to earlier findings by Orihuela-Torres et al. (2022) in a Mediterranean wetland, we found the scavenger assemblage to vary across seasons, whilst the ecological function of carrion removal remained consistent. Studies conducted in other ecosystems found that carrion consumption was higher during winter due to the scarcity of prey and other food sources (Needham et al., 2014; Selva et al., 2005). However, it appears that, in Mediterranean wetlands, this ecological function remains constant throughout the year, possibly due to the high productivity and thus the great diversity of species that these ecosystems harbour, and also because of milder winters than in more northern latitudes. This is also reflected in the high number of scavenger species recorded in Mediterranean wetlands, i.e. 26 species by Orihuela-Torres et al. (2023) and 22 species in our study. These are higher numbers than in most studies of vertebrate scavenger assemblages in other ecosystems worldwide (Sebastián-González et al., 2019). It would be interesting to conduct studies on the structure and functioning of vertebrate scavenger assemblages in wetlands at other latitudes, both tropical and near the poles, to evaluate how they respond to seasons and if there is also this 'functional turnover' throughout the year.

5. Conservation implications

Our results showed the differences in scavenging dynamics between artificial and natural wetlands, highlighting the impact that *wetland* *management* (modification of water surface and hydroperiod) can trigger not only on aquatic organisms, but also on the biodiversity associated with the wetland and its ecological functions. Carrion was consumed much faster in artificial wetlands, due to the higher presence of avian scavengers associated with water surfaces (western marsh harriers and gulls), and it was monopolized by more opportunistic (red fox, gulls, and rodents) and non-native (brown rat) species. However, scavenger species richness was lower in artificial wetlands (e.g., fewer raptors or mesocarnivore species), indicating that artificial wetlands do not replace natural wetlands in terms of biodiversity. This could be caused by the fact that artificial wetlands are more predictable and stable, which might favour more generalist species, thereby reducing the competitive ability of species adapted to the seasonal regimes of natural Mediterranean wetlands. In this regard, the desiccation of natural wetlands has consequences not only at the community level on the species more directly involved (e.g., waterbirds, fishes, amphibians, or macroinvertebrates), but it also impacts an essential ecological process such as carrion consumption, altering nutrient cycling and transport (Parmenter and Macmahon, 2009; Wilson and Wolkovich, 2011), and probably other ecosystem services such as pathogen regulation (Markandya et al., 2008). These functions may become even more essential in the future, as mass mortality events (i.e., appearance of large quantities of carrion concentrated in space and time) in wetlands are increasing in occurrence and magnitude (Fey et al., 2015). Furthermore, human-related activities (e.g., fish farming, littered anthropogenic food waste), as well as a lower presence of potential predators in artificial wetlands, benefits non-native species (Gilby et al., 2023; Orihuela-Torres et al., 2023), which can have serious consequences for the entire wetland ecosystem.

We also observed a much faster consumption, by a greater number of species, of aquatic-origin carrion compared to terrestrial-origin carrion. These findings highlight the crucial role played by vertebrate scavengers in the transport of essential nutrients (such as phosphorus or nitrogen) from water to land and its significant impact in these ecosystems. It would be valuable to study the amount of nutrients mobilised from water to land or vice versa (Martín-Vélez et al., 2019), through 'carcass transport' and the scavengers' egesta and excreta, as well as the effect these nutrients have on the ecosystem (Payne and Moore, 2006).

Although natural wetlands hosted a higher number of vertebrate scavenger species, artificial wetlands exhibited higher efficiency in carrion removal (half the time). During our fieldwork, most natural wetlands were dry or had low water surface area and permanence due to the scarcity of rainfall and the low water table levels, whereas artificial wetlands maintained stable water levels. This was true even during the spring season, when natural wetlands are usually extensively flooded. However, the reduced rainfall paired with water abstraction from aquifers for agriculture and beach tourism has dramatically reduced the amount of water in Doñana, even during periods when the natural wetlands should be completely flooded, and has also altered the terrestrial vegetation around the wetlands (Green et al., 2024). However, the wider impacts on ecosystem functioning are still unknown. Our study shows that, not only are many natural wetlands drying up (Camacho et al., 2022; Green et al., 2024), but essential ecosystem services provided by scavengers are also being lost. Likely, this water 'kidnapping' is negatively impacting other ecological functions provided by fauna, such as seed dispersal or pollination, and this warrants further investigation in future studies. Therefore, it is urgent to regulate the amount of water that can be extracted from the aquifers to maintain minimum groundwater levels that ensure the functionality of this important wetland complex and the ecosystem services it provides us.

Based on our results, artificial wetlands, particularly those dedicated to conservation, should emulate natural dynamic hydrological cycles. This would promote the recovery of ecological functions, the resurgence of native species adapted to these cycles, and help prevent the proliferation of invasive species, e.g., the common carp. However, if the recharge of aquifers in Doñana is not restored, aligning the management of artificial wetlands with natural hydrological regimes could be detrimental to the system. Our findings suggest that these artificial wetlands currently play a vital complementary role in maintaining ecological functions and serve as critical refuges for numerous species, especially as drought periods become increasingly frequent (García-Ruiz et al., 2011).

CRediT authorship contribution statement

Adrian Orihuela-Torres: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Juan Manuel Pérez-García:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Eneko Arrondo:** Writing – review & editing, Writing – original draft, Methodology. **Tatiana Pessano-Serrat:** Writing – review & editing, Visualization, Methodology. **Andy J. Green:** Writing – review & editing. **Lara Naves-Alegre:** Writing – review & editing, Methodology. **Francisco Botella:** Writing – review & editing, Methodology. **Nuria Selva:** Writing – review & editing. **José Antonio Sánchez-Zapata:** Writing – review & editing, Methodology. **Esther Sebastián-González:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data available via figshare doi:https://doi.org/10.6084/m9.figshare.25858660.v1

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110929.

Data availability

I have shared the link to my data

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