



# Rice fields play a complementary role within the landscape mosaic supporting structurally and functionally distinct waterbird communities

João Paulino · José Pedro Granadeiro ·  
Paula Matos · Teresa Catry

Received: 20 February 2024 / Revised: 20 September 2024 / Accepted: 21 September 2024  
© The Author(s) 2024

**Abstract** This study aims to understand how the structure and functions of waterbird communities in rice fields compare to those in other habitats within an agricultural landscape encompassing five habitats: saltpans, lakes, intertidal areas, pastures and rice fields. Over 2 years, waterbird counts were conducted every 15 days in these habitats. Non-metric multidimensional scaling was used to compare the composition and functional structure of the waterbird communities. Differences in both metrics were found among habitats throughout the year. These appear to be driven by spatial (presence of permanent water cover) and temporal gradients (yearly seasonality). Rice fields occupy a central position within the gradients. The composition and functional structure of

waterbird communities in rice fields undergo significant changes throughout the year associated with the annual rice production cycle. Other habitats maintain more consistent communities, reflecting their more stable environmental conditions. Rice fields play a complementary role to other habitats in the landscape, likely acting as a buffer, partially mitigating the loss of some waterbird species amid the global decline of natural wetlands.

**Keywords** Agricultural systems · Rice cycle · Wetlands · Functional diversity · Ecosystem services

## Introduction

Wetlands cover approximately 5 to 8% of the earth's surface (Mitsch & Gosselink, 2000; Mitsch & Mander, 2018; Xu et al., 2019) and are one of the most productive environments worldwide, holding high biological diversity, providing water and being a source of primary productivity, crucial for a large number of animal and plant species (Yoon, 2009). Yet, wetlands are among the world's most endangered habitats, with a recorded decrease in area of over 20% in the last 400 years (Ballut-Dajud et al., 2022; Fluet-Chouinard et al., 2023). In parallel with the loss of natural wetlands, artificial wetlands are increasing in many regions (Yoon, 2009; Ramsar Convention Secretariat, 2010). Rice (*Oryza* sp.) fields are the second largest wetland type worldwide and the largest

---

Handling editor: Stuart Halse

---

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10750-024-05709-w>.

---

J. Paulino (✉) · J. P. Granadeiro · T. Catry  
Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Centro de Estudos do Ambiente e do Mar (CESAM), 1749-016 Lisbon, Portugal  
e-mail: joaoc215@gmail.com

P. Matos  
Laboratório Associado TERRA, Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território, Universidade de Lisboa, 1600-276 Lisbon, Portugal

irrigated crop (International Rice Research Institute, 1995; Ramsar Convention Secretariat, 2010) as rice is the primary food for almost 50% of humanity (Seck et al., 2012).

Rice fields often provide valuable habitat for wildlife, in particular for waterbirds that forage in these areas during the whole breeding and/or non-breeding seasons or for shorter stopover periods during their migratory journeys (Fasola & Ruiz, 1996; Elphick, 2000; Lourenço & Piersma, 2009; Lourenço et al., 2010; Parejo et al., 2019). Consequently, many areas comprising rice fields around the world have been classified as Important Bird and Biodiversity Areas (IBAs) by BirdLife International and are listed as Ramsar sites (Elphick et al., 2010). However, the contribution of rice field habitats to waterbird conservation remains poorly understood (Yoon, 2009; Ramsar Convention Secretariat, 2010). Adding to this discussion, there is growing concern that rice crops can act as ecological traps by attracting birds to these dynamic and short-lived habitats which may become unsuitable during a significant part of the year (Elphick, 2015).

The main threats in these areas for birds are changes to the habitat structure due to alterations in management practices or abandonment (Fasola & Ruiz, 1996; Elphick, 2015; Katayama et al., 2020), the risk of contamination with pesticides (Parsons & Mineau, 2010; Henriques et al., 2014) and destruction of nests due to changes in the inundation schedule or hydrological conditions (Pierluissi, 2010; Herring et al., 2021). Moreover, although a large number of waterbirds use rice fields, how waterbird community structure and functioning in rice fields compares with other natural and artificial wetlands is still poorly known. This comparison is hampered by the fact that rice fields are very seasonal habitats, undergoing sudden changes across the cycle of rice cultivation that may change their suitability for different waterbird species due to changes in food availability and accessibility. Paddies have no rice growing for part of the year (Lourenço & Piersma, 2009) and, when there is no rice in the fields, the paddies may be left with standing stubble or be ploughed (Lourenço & Piersma, 2009). Moreover, water management may also change over the year, depending on the region of the world: paddies are kept flooded during the rice cultivation period but after harvest the water levels may vary depending on precipitation or be managed

to keep a specific level (Lourenço & Piersma, 2009). All these management actions create a strong temporal dynamic of food availability for waterbirds. Over the year, rice fields have different available food sources for the waterbird community including fish (Clavero et al., 2015), amphibians (Ribeiro et al., 2019) and invertebrates (Leitão et al., 2007; Henriques et al., 2014; Clavero et al., 2015) in flooded fields. Also, birds can consume rice directly from the plant (Toral et al., 2012) or rice leftovers after harvest (Lourenço & Piersma, 2009). As a consequence, the importance of rice fields for different waterbird species may change over the year.

To assess the importance of rice fields for waterbird communities, it is critical to compare the structure, functioning and temporal dynamics of the waterbird community using rice fields with those using other types of wetland. For this comparison, it is important to look at the waterbird community both in terms of species composition and abundance, but also functional trait composition. While the first gives insight into the importance each habitat has for different waterbird species (Hooper et al., 2005; Coelho et al., 2021), the second shows whether, regardless of species composition, the functions performed by waterbirds are similar among habitats (Naeem & Wright, 2003; Hooper et al., 2005; Díaz et al., 2007). The functional diversity of a community is a crucial aspect of biodiversity (Díaz & Cabido, 2001) and understanding species' functional traits is crucial for grasping the community functional structure and, thus, its influence on the environment (Mouillot et al., 2013; Kraft et al., 2015). One of the most relevant components of the functional structure of communities is dominant trait values, often expressed by the Community Weighted Mean (CWM), i.e. the average of functional traits weighted by their relative abundances in the community (Garnier et al., 2004). Several studies have demonstrated systematic variation of CWM of traits along abiotic gradients and between different habitats (e.g. Wright et al., 2004; Cornwell and Ackerly, 2009; Sonnier et al., 2010). Hence, this index presents itself as ideal to compare the functional structure of the waterbird community in rice fields and in other habitats.

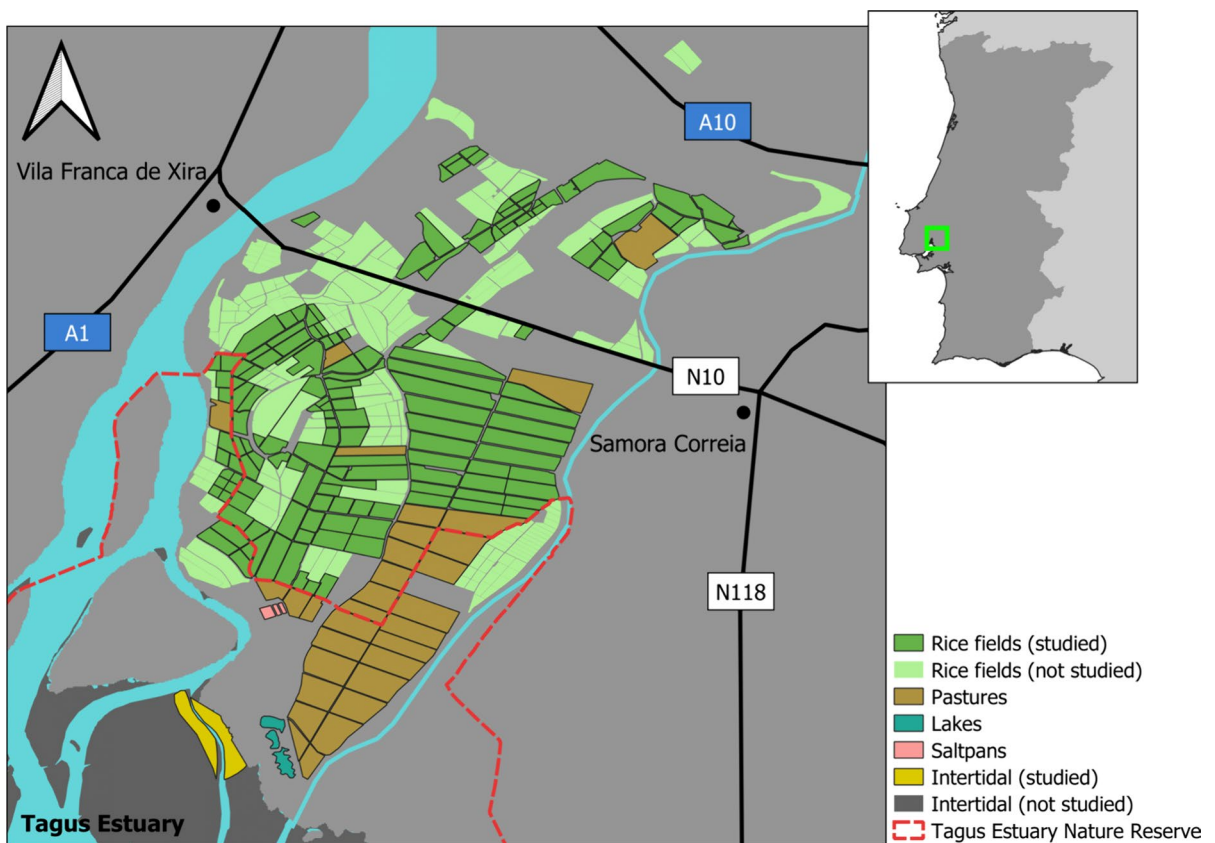
In this study, we aim to understand how the structure and functions of the waterbird community in rice fields compare to those in the surrounding landscape, namely in other artificial and natural wetlands.

The study area is adjacent to the Tagus River estuary (Portugal), an area that holds internationally important numbers of waterbirds, and comprises both natural and artificial wetlands, including rice cultivations (e.g. Delany et al., 2009; Lourenço and Piersma, 2009; Parejo et al., 2019), lakes, salt pans, intertidal areas and pastures. Given the high seasonality of rice fields, associated with the annual cycle of rice production, the study was conducted across the whole year. Ultimately, this information is crucial to understand whether rice fields can serve as alternative habitats for waterbirds in the worldwide scenario of natural wetland loss.

## Methods

### Study area

The study area consisted of an agricultural landscape surrounded by large areas of saltmarsh and intertidal mudflats of the Tagus River basin ( $38^{\circ} 57' N$ ,  $8^{\circ} 54' W$ ) known as Lezíria Grande near the town of Vila Franca de Xira, Portugal (Fig. 1). This landscape, covering 14,563 ha, is composed of estuarine waters, mudflats, saltmarshes, river islands, pastures and agricultural land where different crops are cultivated, most predominantly rice. This area has a high biological significance and the estuary, intertidal areas and southernmost part of Lezíria Grande, including some rice fields and pastures, have been listed as an Important Bird and Biodiversity Area by ICBP, since 1989, and BirdLife since 2000, and as a Natural Reserve (1976) and a Ramsar site (1980) and, together with the remaining rice fields in the study



**Fig. 1** Study area. Map showing the study area including all habitats surveyed in Lezíria Grande

area, as a Special Protection Area since 1994 under Natura 2000 network.

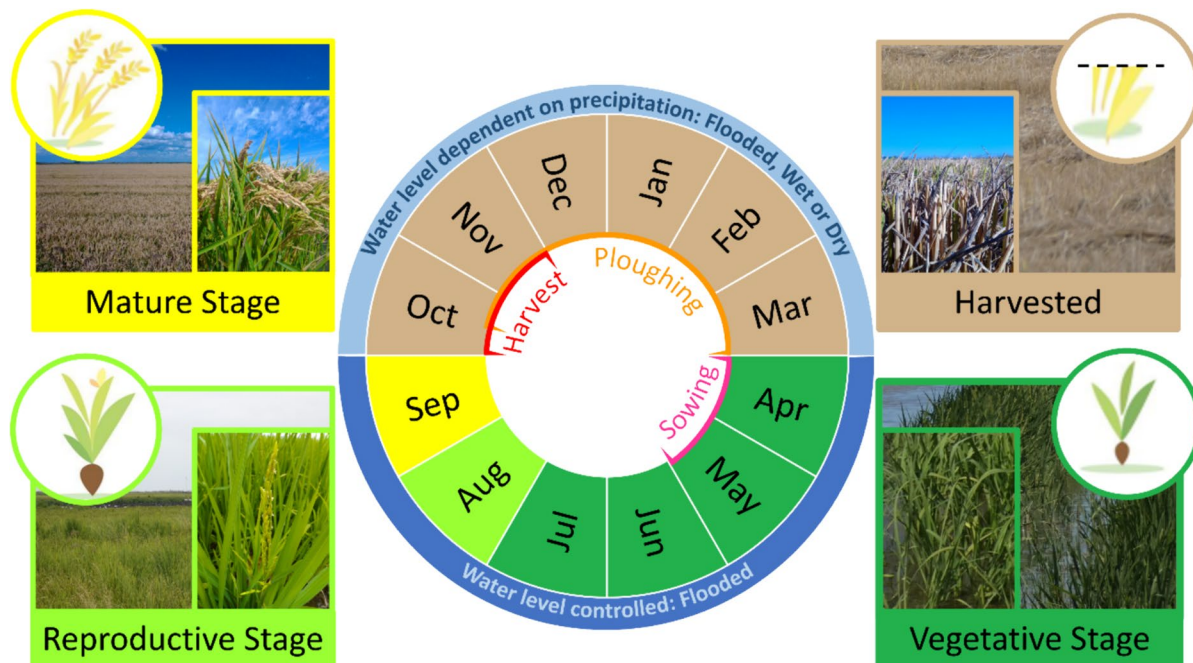
The area selected for the study includes both artificial and natural wetlands in Lezíria Grande, and pastures (1325 ha). Artificial wetlands include mainly rice fields (2665 ha), but also saltpans (11 ha) and artificial lakes (33 ha), while natural wetlands are represented by intertidal mudflats (297 ha). For the purpose of this study, we will refer to each of the five aforementioned environments as “habitats” for water-bird communities.

The rice fields in Lezíria Grande support the largest contiguous area of rice in the Tagus River basin and one of the largest in Portugal. This production is of special importance since it is cultivated with methods targeting the least ecological impact. Rice produced in this area was awarded a Protected Geographical Indication (IGP) in 2006. No pesticides are used, only selective, biodegradable herbicides (Iken, 2017).

The annual rice cycle stages include vegetative, reproductive, mature and harvested (Nelson et al., 2014). In the study area, sowing occurs early in the spring (April–May). During this period the paddies are flooded to allow for the seeds to germinate. Soon

after, the water levels are allowed to drop so that the rice seedlings can take root. Afterwards, the paddies are flooded again, and the water levels are kept high for most of the growing period. By the end of the summer (September), the rice is maturing, and the water levels are allowed to drop until the fields are mostly dry in time for the harvest, taking place in October and November. From November to April, there is no rice cultivation and the water levels on the rice paddies are not controlled and depend mostly on precipitation (Lourenço & Piersma, 2009). All paddies are ploughed and levelled during this period. These management actions are done mainly between October and December and are mostly finished by early February. A schematic of the typical yearly cycle of rice cultivation in the study area is shown in Fig. 2. All stages of rice production were considered for this study.

Pastures in the study area are used for livestock production and are managed targeting high productivity which includes yearly ploughing, manuring and sowing of grass and legumes. These lands are then occupied by cattle and horses intermittently over the year to allow for fallow. The pastures are mostly dry



**Fig. 2** Cycle of rice production. Typical schedule of the yearly cycle of rice production in Lezíria Grande including the stage of rice production (vegetative, reproductive, mature and harvested), water level and management actions (sowing, harvest and ploughing)

over the year although they are surrounded by a complex system of irrigation ditches that have water year-round. Yet, after heavy rain, the pastures may become flooded and resemble a marsh for several days or weeks.

The artificial lakes included in this study are located in the southwestern part of the study area, cover ca. 33 ha and are managed by the Space for Visitation and Observation of Birds (EVOA). The area is managed with the aim of offering high-tide refuge, nesting grounds and foraging areas to waterbirds, namely those inhabiting the Tagus estuary. The salt pans surveyed in this work (Saragoça salt pans) are abandoned and the water level depends mostly on precipitation. These salt pans attract large numbers of birds seeking high-tide refuge.

### Waterbird counts

Waterbirds were counted approximately every 15 days between 28-Apr-2021 and 13-Apr-2023 in the selected habitat patches, using binoculars and telescope. In total, 48 counts were performed in each of the five habitats in this period. Waterbirds include all birds belonging to the orders Anseriformes, Ciconiiformes, Charadriiformes, Galliformes, Gruiformes, Pelecaniformes and Phoenicopteriformes. Some bird species belonging to these orders that are usually not considered waterbirds (such as lapwing, *Vanellus vanellus* (Linnaeus, 1758), cattle egret, *Bubulcus ibis* (Linnaeus, 1758), etc.) have also been included in the study due to their strong association with freshwater habitats in the study area. Counts were categorized according to habitat type. Waterbirds were counted in the rice fields and pastures using a network of tracks to access different fields by car. In contrast, for salt pans, lakes and intertidal area counts were performed from one or several stationary counting points allowing the coverage of the predefined study areas. The intertidal counts differed only in the fact that they were performed hourly from a stationary point in the period of 2 h before and after low tide peak. In all habitats, the observer continued counting until no new species were detected for five minutes. Each rice paddy, pasture paddock, lake unit and salt pan tank was counted individually (the sum of all waterbirds in each habitat for each count was then used). All habitats were counted within the same week. Usually rice fields and pastures were counted in one day

(7 to 12 h count duration), while lakes and salt pans were counted at high and low tide peak in the same day (the average of the two counts was then used for these habitats).

Night counts were also performed in the rice fields since some species (mainly ducks and flamingos) preferentially forage there during the night and could therefore be underestimated if only diurnal counts were performed. These counts were performed in the same week as the diurnal counts, for 1 h after sunset, using binoculars and a telescope, from a vantage point that allowed for all birds entering the rice fields coming from the estuary to be detected and counted. Night counts were not performed in any other habitats because, after conducting multiple rounds of test counts, no significant influx of night foragers was observed in pastures, salt pans, lakes, or intertidal areas, whereas large numbers of birds (mainly ducks and flamingos) were seen entering the rice fields.

### Functional trait compilation

For each bird species recorded in the study area, twenty-four functional traits were collected using AVONET (Tobias et al., 2022) and EltonTraits 1.0 (Wilman et al., 2016), two free databases containing comprehensive functional trait data for all birds (Table 1). The traits selected for this study were chosen given their high probability to respond to differences in land use or habitat type (Hevia et al., 2017) and thus being the most likely to be linked to the differences between habitat types in this study.

### Data analysis

Within each habitat type, counts were classified according to the stage of the cycle of rice production (period): vegetative (April to July; 14 counting events), reproductive (August; four counting events), mature (September; four counting events), harvested I (October to November; eight counting events), harvested II (December to February; 10 counting events) and harvested III (February to April; eight counting events). The harvested stage was divided into three periods since it spans close to 6 months every year encompassing many changes in the bird community over all the habitats that could be lost if analysed together. In total, 240 counts (48 counts in each of five habitats) were analysed. Counts were converted

**Table 1** Traits used to measure waterbird functional diversity

Trait	Variable type	Categories	References
Mass (g)	Continuous	–	Tobias et al. (2022)
Beak length (culmen, mm)	Continuous	–	Tobias et al. (2022)
Beak length (nares, mm)	Continuous	–	Tobias et al. (2022)
Beak width (mm)	Continuous	–	Tobias et al. (2022)
Beak depth (mm)	Continuous	–	Tobias et al. (2022)
Tarsus length (mm)	Continuous	–	Tobias et al. (2022)
Wing length (mm)	Continuous	–	Tobias et al. (2022)
Kipps' distance (mm)	Continuous	–	Tobias et al. (2022)
Secondary 1 length (mm)	Continuous	–	Tobias et al. (2022)
Hand-wing index <sup>a</sup> (adimensional)	Continuous	–	Tobias et al. (2022)
Tail length (mm)	Continuous	–	Tobias et al. (2022)
Trophic level	Categorical	Carnivore Herbivore Omnivore	Tobias et al. (2022)
Trophic niche	Categorical	Aquatic predator Granivore Aquatic herbivore Terrestrial herbivore Invertivore Generalist	Tobias et al. (2022)
Migratory behaviour	Categorical	Migratory Partially Migratory Sedentary	Tobias et al. (2022)
Invertebrate diet (%)	Continuous	–	Wilman et al. (2016)
Vertebrate diet (%)	Continuous	–	Wilman et al. (2016)
Scavenger (%)	Continuous	–	Wilman et al. (2016)
Fruit diet (%)	Continuous	–	Wilman et al. (2016)
Plant diet (%)	Continuous	–	Wilman et al. (2016)
Time spent foraging underwater (%)	Continuous	–	Wilman et al. (2016)
Time spent foraging in the water surface (%)	Continuous	–	Wilman et al. (2016)
Time spent foraging in the ground (%)	Continuous	–	Wilman et al. (2016)
Time spent foraging in the understory (%)	Continuous	–	Wilman et al. (2016)
Time spent foraging in the air (%)	Continuous	–	Wilman et al. (2016)

<sup>a</sup>Hand-Wing Index: a morphological metric linked to wing aspect ratio. Here it is defined as  $100 \cdot \text{KD} / \text{WL}$ , where KD is Kipps' Distance (the distance between the tip of the first secondary feather and the tip of the longest primary feather) and WL is Wing Length (see Lockwood et al., 1998)

into relative abundance for each bird species in each habitat. For the intertidal habitat, all counts performed in the same day were first averaged and then transformed into values of relative abundance.

All morphological traits that consisted of linear body measures were corrected for mass by dividing each value by the cubic root of the mass. Species abundance was combined with species trait data to obtain the community-level weighted mean (CWM) (Lavorel et al., 2008). This index represents the mean

trait value in the community, weighted by the abundance of species having those values (Lavorel et al., 2008). In the case of categorical traits, the CWM represents the mean for each functional group belonging to that trait weighted by the abundance of species from the same trait (i.e. it is the proportion of species having belonged to a species functional group weighted by abundance in relation to the rest of the functional groups of that trait). This index was calculated using the 'dbFD' function of the FD package

(Laliberte & Legendre, 2010; Laliberté & Legendre, 2014), running in RStudio (R Core Team, 2022).

To examine the species composition of the waterbird community and represent the abundance of each species in each habitat, two network biplots were created using the function ‘*plotweb*’ in the R package *bipartite* (Dormann et al., 2008) connecting all species counted in the study area to each of the five habitats they use. The width of the links represents the average abundance over the year of a species in a habitat.

To detect prominent differences in species composition across habitats, we performed a non-metric multidimensional scaling (NMDS) ordination on a matrix of counts across all habitat types by species relative abundance, using the R package *vegan* (Okasen et al., 2013) (function ‘*metaMDS*’). The Bray–Curtis distance measure was used for the NMDS analysis, as it has been shown to be one of the most effective measures of species dissimilarities and, therefore, recommended for community data (McCune et al., 2002). To build the NMDS, data underwent 10,000 iterations per run, and the best (lowest stress) solution from 10,000 runs with real data was chosen, each run beginning with a random configuration. The NMDS is a method for nonlinear mapping, as such, contrary to PCA, PCoA, or CA, which are eigenvector-based methods, NMDS calculations do not maximize the variability associated with individual axes of the ordination and the concept of variation explained is not usually applied (Legendre & Legendre, 2012). However, 1-stress<sup>2</sup> transforms nonlinear stress into a quantity analogous to the squared correlation coefficient and, thus, variation explained. Therefore, the variation explained by each axis of our NMDS ordinations was calculated using the function ‘*stressplot*,’ which displays the nonlinear fit and gives this statistic.

Scaled, but not centred, CWM values for each functional trait were overlaid in the species NMDS ordination plot as a set of environmental vectors, calculated using the ‘*envfit*’ function in the *vegan* package. After overlaying this first set of vectors, the CWM variables were inspected for collinearity. Whenever two CWM variables were found to have a high Pearson correlation ( $R^2 > 0.8$ ), the one whose vectors had the lowest correlation with the species NMDS ordination axes was discarded. Moreover, because we were only interested in investigating the

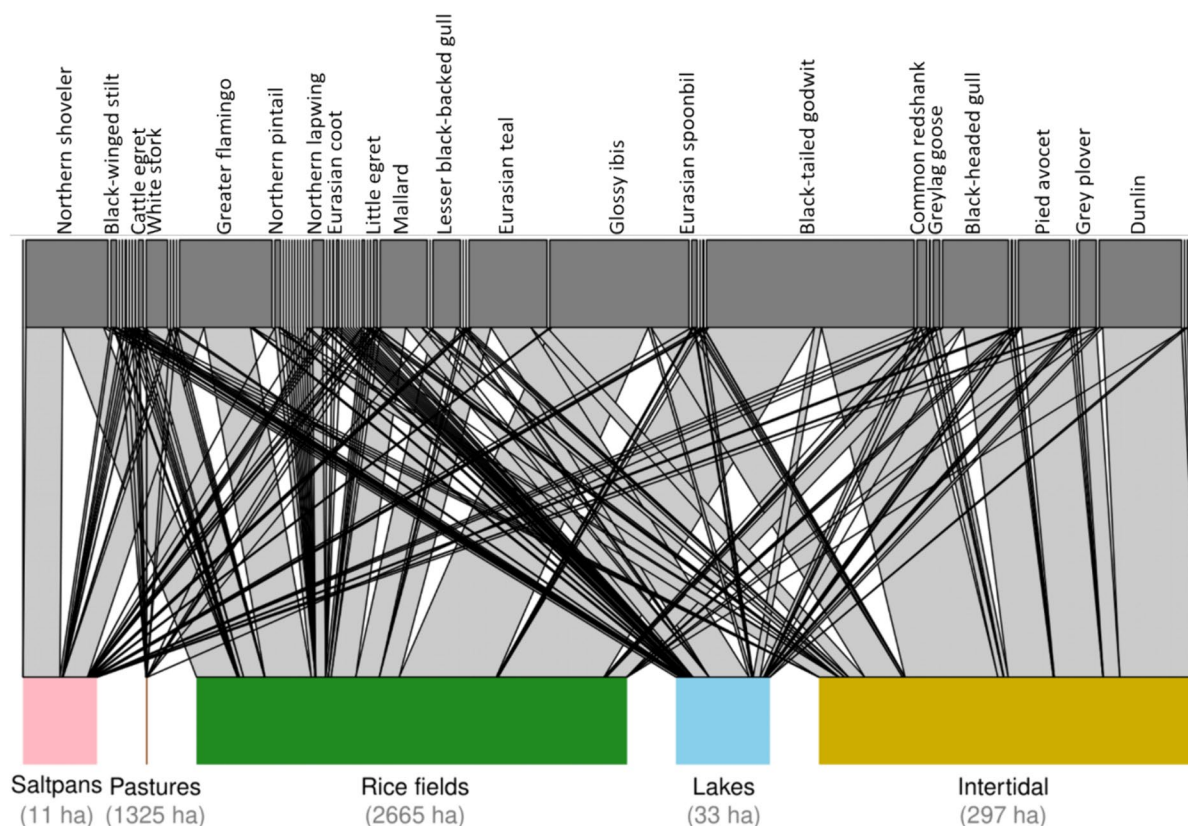
traits mediating species response among these habitats and with time, only the CWM vectors with significant correlation with axes of interest ( $R^2 > 0.2$  and  $P$  value  $< 0.05$ ) were considered relevant and discussed, the others were discarded. This final selection of variables was then used to perform an NMDS on a matrix of trait CWMs per period across all habitat types to detect prominent differences in functional structure across habitats following the same procedure described above.

To understand how similar rice fields are to the other four habitats (lakes, saltpans, intertidal areas and pastures) in terms of species composition and functional structure across the yearly cycle of rice production, for each period, we calculated the mean Euclidean distance between rice field points (coordinates) in the NMDS ordinations described above, and the points of the other habitats. The significance of the differences between (1) the mean distance from rice fields to other habitats within each period and (2) the mean distance between rice fields and each other habitat over the stages of the cycle of rice production was assessed using an ANOVA followed by Tukey post hoc tests with adjusted  $P$  values.

## Results

Species composition of waterbird communities in rice fields and surrounding habitats across the year

A total of 69 waterbird species were recorded in the study area. Lakes were the richest habitat, with 53 species, followed by rice fields with 52, intertidal areas with 39, saltpans with 35 and finally pastures with 14 species. The density of the most abundant waterbird species over the year in each habitat can be found in Online Resource 1. Most habitats were dominated by only a few species with one to three species contributing over 50% of the overall abundance (Fig. 3). Across the year, rice fields were dominated by black-tailed godwit, *Limosa limosa* (Linnaeus, 1758) and glossy ibis, *Plegadis falcinellus* (Linnaeus, 1766), each contributing to about 25% of the bird abundance, followed by greater flamingo, *Phoenicopterus roseus* Pallas, 1811, and northern shoveler, *Anas clypeata* Linnaeus, 1758, each contributing about 10%. Moreover, 97% of the white stork, *Ciconia ciconia* (Linnaeus, 1758), were counted in rice fields.



**Fig. 3** Network biplot showing the links between the waterbird species counted in the study area and the five different habitats. The width of the links represents the average abundance of a species in each habitat calculated for the whole

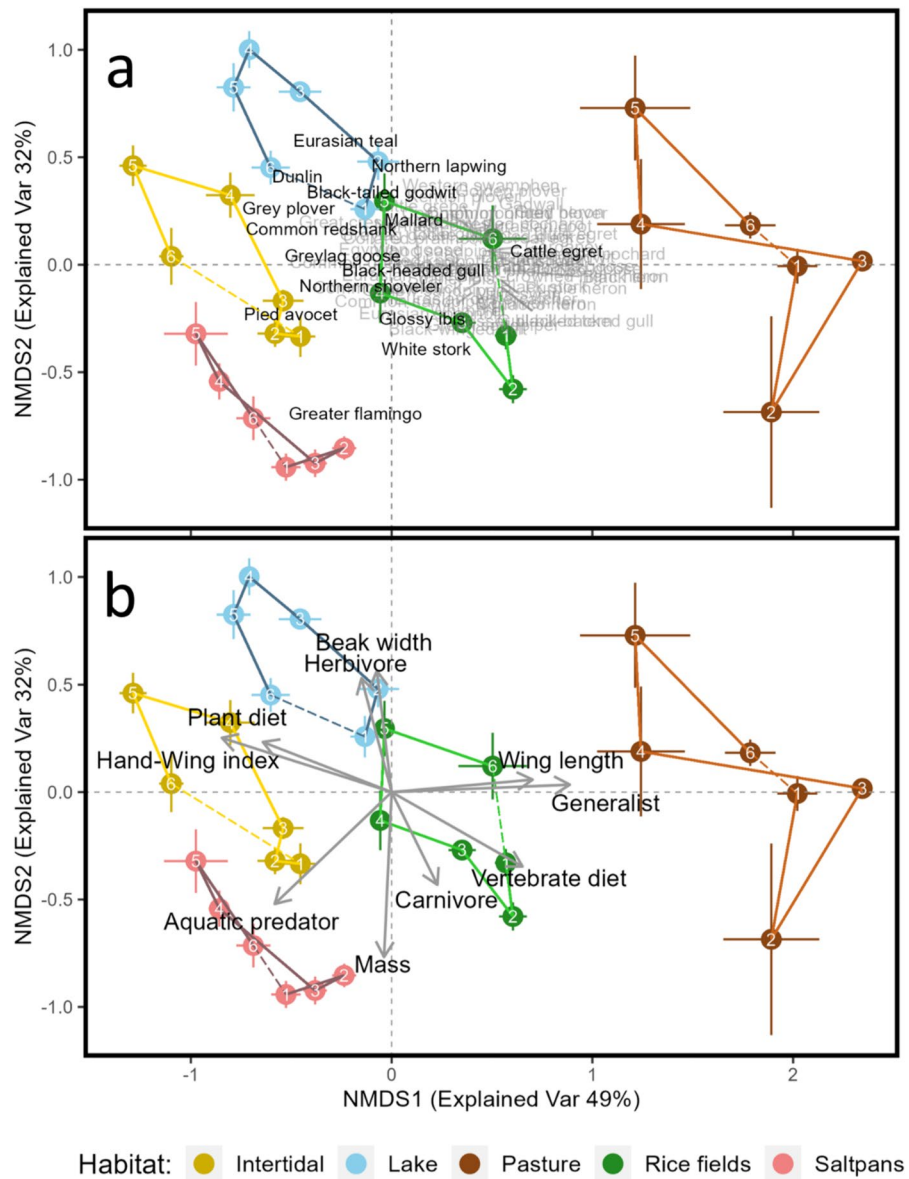
The dominant species in lakes were the Eurasian teal, *Anas crecca* Linnaeus, 1758, and mallard, *Anas platyrhynchos* Linnaeus, 1758 (relative abundance: 43% and 17% respectively). In intertidal areas, black-tailed godwit (24%) and dunlin, *Calidris alpina* (Linnaeus, 1758) (21%), followed by pied avocet, *Recurvirostra avosetta* Linnaeus, 1758 (10%), black-headed gull, *Larus ridibundus* Linnaeus, 1766 (10%), and glossy ibis (10%) were the most abundant species. Saltpans were dominated by two species over the year, greater flamingo, and northern shoveler (relative abundance: 33% and 50%, respectively). Finally, bird numbers in the pastures were headed by cattle egret (40%), black-headed gull (10%), northern lapwing (10%), white stork (10%) and mallard (10%, Fig. 3).

The NMDS ordination joint plot (Fig. 4) shows the centroids of all counts of species composition for each period in each habitat (the joint plot showing

study period. Despite all bird species being represented, only the species with over 5% contribution for at least one habitat are named

all counts can be found in Online Resource 2). This analysis suggested three dimensions (the addition of a fourth dimension had only a slight reduction in minimum stress) with a final stress of 0.03. As the first two axes seem to depict the gradients of interest, also having the highest values of variation explained, the third axis will not be further discussed. The first axis shows a habitat gradient, with rice fields located at an intermediate position between a group formed by habitats with permanent presence of water (intertidal mudflats, lakes and saltpans) in one side, and mostly dry pastures on the other side. This axis also suggests the separation of habitats with more (rice fields, pastures) and less (intertidal mudflats, lakes and saltpans) dynamic environmental conditions across the year, resulting from different levels of human intervention/management. Overall, the non-overlapping centroids ( $\pm$ SE) suggest that distinct waterbird communities

**Fig. 4** Non-metric multidimensional scaling (NMDS) analysis of species composition of waterbird communities using values of relative abundance. Points represent the centroids ( $\pm$  SE) of counts performed in each habitat during each stage of the cycle of rice production (1—vegetative, 2—reproductive, 3—mature, 4—harvested I, 5—harvested II and 6—harvested III). Each centroid is chronologically connected to the next by a segment. Final stress = 0.03. **a** ordination showing species names. Species summing up around 50% of abundance in each habitat are represented by black names, while grey names represent less abundant species; **b** overlay with vectors representing significant correlations between community composition and community weighted mean (CWM) of the functional traits. Only vectors with a significant correlation with the ordination ( $P < 0.05$ ) and an  $R^2 > 0.2$  are represented



inhabit each habitat at each period. The second axis portrays a temporal gradient related to seasonality, with habitats in the positive side of the axis mostly dominated by migratory species, and those in the negative side hosting mainly resident species. This seasonality is well marked in each habitat, and therefore, each of them shows higher scores during the wintering period (harvest I and especially harvest II), when migratory species are more abundant and lower scores in the rest of the year.

The distribution of most species does not follow a clear pattern along the first axis, as they appear

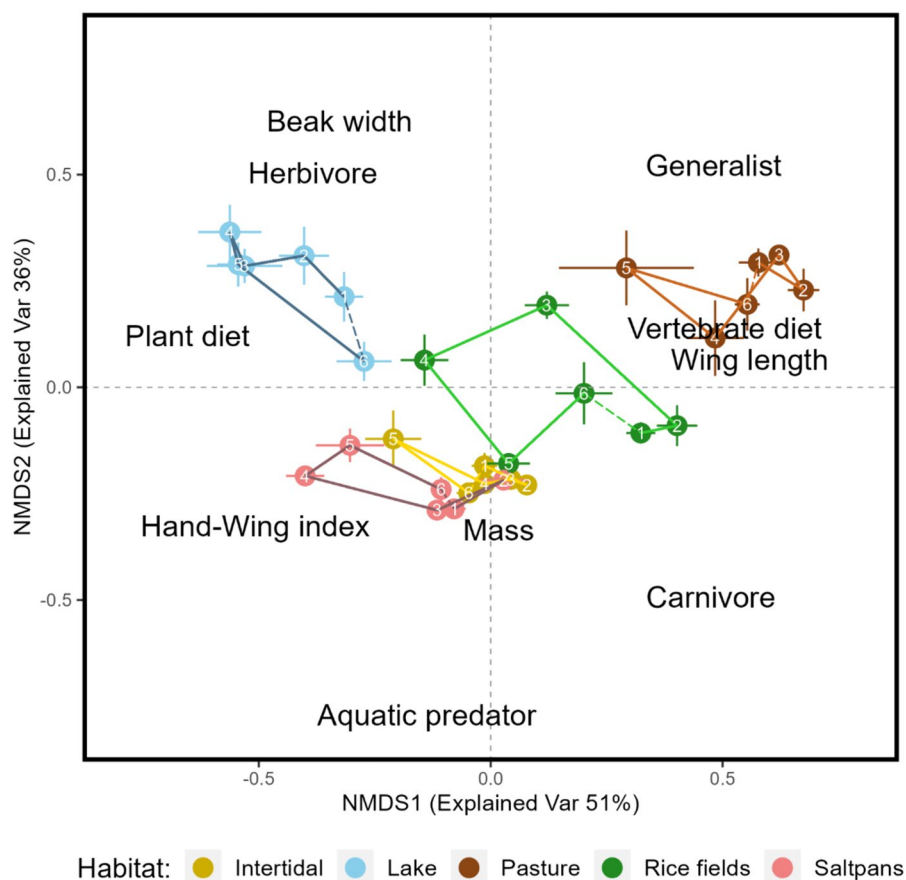
mostly clustered along its central part. Nevertheless, if we focus on the most dominant species (i.e. summing up around 50% of abundance) of each habitat, then greater flamingo, dunlin, common redshank, grey plover, greylag goose and pied avocet appear more associated to the negative side of the axis (associated with permanent aquatic habitats), cattle egret to the positive side (associated with pastures) and northern lapwing, black-tailed godwit, mallard, black-headed gull, northern shoveler, glossy ibis and white stork clustered at the middle of the axis (associated with rice fields; Fig. 4a).

The CWM of traits and functional groups with significant correlations with the first and second axis were overlaid in the ordination as vectors (Fig. 4b). From the set of 24 traits, eight seem to be reflecting bird species response to the habitat and time gradients (mass, beak width, wing length, hand-wing index, trophic level, trophic niche, % vertebrate diet and % plant diet). Species that feed on plants, aquatic predators and with a high hand-wing index were associated with more stable habitats with more presence of water, while generalist species, vertebrate consumers and species with higher wing length were associated with more dynamic habitats where water is not present year-round in their entire area, i.e. rice fields and pastures. On the other hand, herbivore species and species with wide beaks occurred mostly in autumn/winter season (October to April), while aquatic predators, carnivores, birds with vertebrate diet and heavier birds were more frequent in spring/summer, the rice growing season (April to September).

Functional structure of waterbird communities in rice fields and surrounding habitats across the year

The NMDS ordination joint plot (Fig. 5) shows the count centroids of trait CWM for each stage of rice development in each habitat (see also Online Resource 3, depicting all counts). The ordination suggested three dimensions with a final stress of 0.05. Once again, only the first two axes will be discussed. The results obtained were concordant with those of the NMDS analysis produced with values of waterbird abundance. The first axis suggests the same habitat gradient, with rice fields in a central position. As in the previous analysis, the second axis seems to partly represent a temporal gradient. Yet the pattern is more complex, probably due to a combination of factors including season and income of migratory species. This second axis shows a group formed by lakes and pastures on the positive side and intertidal areas and saltpans on the negative side, with rice fields in the centre. The centroids

**Fig. 5** Non-metric multidimensional scaling (NMDS) analysis of the functional structure of waterbird communities using values of community weighed mean (CWM) for traits. The points represent the centroids ( $\pm$  SE) of sites, i.e. counts performed in each habitat during each stage of the cycle of rice production (1—vegetative, 2—reproductive, 3—mature, 4—harvested I, 5—harvested II and 6—harvested III). Each centroid is connected to the next chronologically by a segment. Names represent the traits used to build the ordination. Final stress = 0.05



of each habitat in each rice cycle stage suggest that each waterbird community in a different habitat has a distinct functional structure at each temporal stage with the exception of the intertidal areas and salt-pans, which show large overlap all year-round.

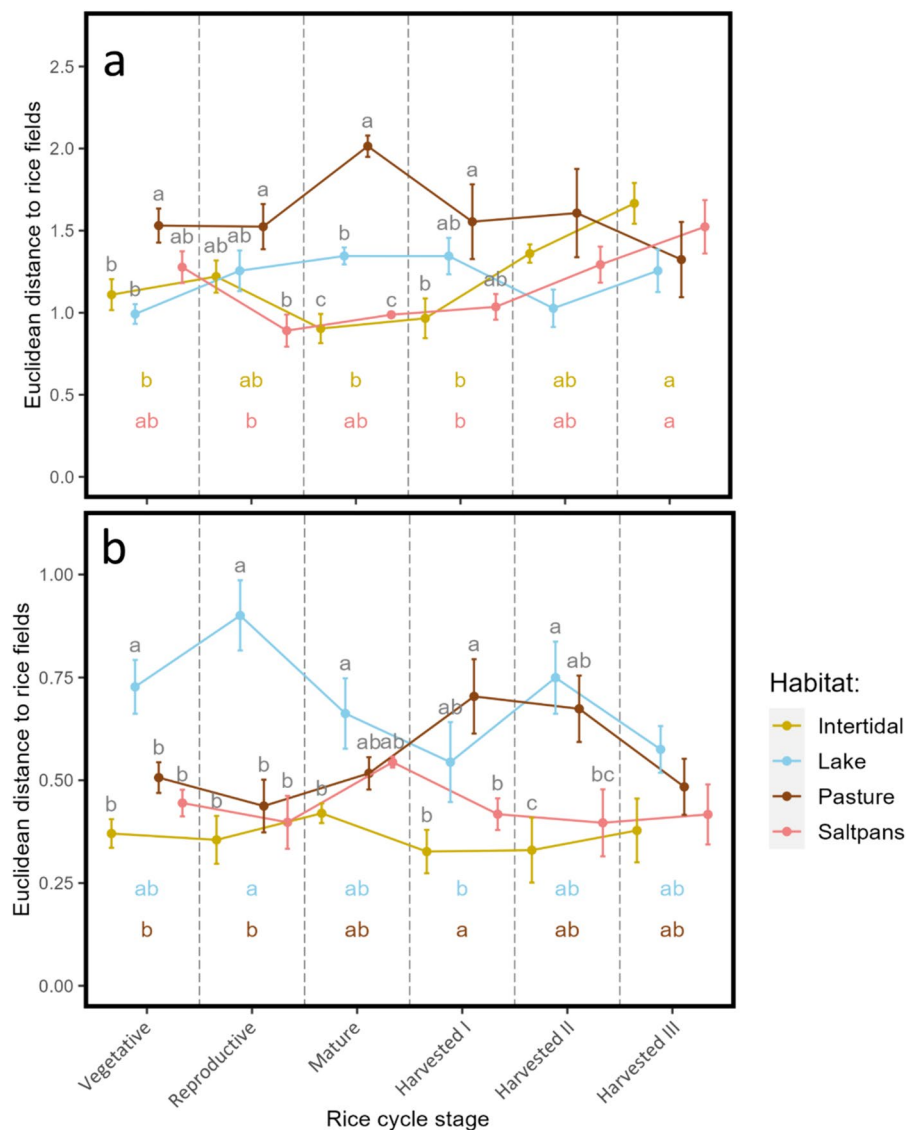
The eight traits and functional groups used to build the ordination in Fig. 5 seem to respond to the habitat gradient. Herbivore species, plant consumers, aquatic predators and species with a high hand-wing index were associated with permanent aquatic habitats, while generalists, vertebrate consumers, carnivores and species with higher wing lengths

were associated with more dynamic habitats, i.e. rice fields and pastures.

Difference between waterbird communities in rice fields and on surrounding habitats across the year

Figure 6 shows how the composition and functional structure of the waterbird community of rice fields compare with those of the remaining habitats across the annual cycle of rice production. The Euclidean distance on the NMDS space between rice fields and any other habitat is significantly higher than zero in all stages, suggesting that the

**Fig. 6** Euclidean distance between rice fields and other habitats. Mean Euclidean distance ( $\pm$  SE) between the non-metrical multidimensional scaling (NMDS) coordinates of waterbird counts performed in rice fields and counts performed in intertidal areas, lakes, pastures and saltpans in the six different stages of the annual cycle of rice production. NMDS ordination was performed using values of: **a** waterbird relative abundance; **b** trait community weighted mean (CWM). The significance of the difference between means was assessed using an ANOVA followed by Tuckey post hoc tests (with adjusted *P* values). Habitats within each stage of the rice cycle not sharing letters (in grey at the top) are significantly different from each other ( $P < 0.05$ ). Rice cycle stages within the same habitat not sharing letters (different colours at the bottom) are significantly different from each other ( $P < 0.05$ ; only the letters relating to habitats that have shown any differences over the rice cycle stages are presented)



waterbird community of rice fields is indeed different from all other habitats over the entire cycle of rice production. In terms of waterbird community composition, pastures present the greater differences relative to rice fields over the rice cycle (Fig. 6a). Both pastures and lakes keep the same distance from rice fields over the year, while intertidal areas and saltpans get closer in the period between the mature and harvested I stage (September to November), suggesting more similar waterbird communities between these habitats and rice fields during this period (Fig. 6a). Globally, in terms of functional structure of the waterbird community, lakes and pastures present the greater differences relative to rice fields all year-round, although there are stages when this distance decreases significantly (Fig. 6b). Lakes differ more from rice fields during the vegetative and reproductive stages (April to August) (Fig. 6b). Pastures seem to follow the opposite pattern of that recorded for the lakes. The differences between pastures and rice fields in terms of functional structure are maximum during the harvested I and II stages (October to February) (Fig. 6b). Intertidal areas and saltpans are the habitats closest to the rice fields during all year suggesting greater similarity in functional structure (Fig. 6b).

## Discussion

Results of this study suggest that rice fields occupy a central position in the habitat gradient of the study area being closer in terms of bird species composition and functional structure to intertidal areas, saltpans and artificial lakes and more distinct from pastures over the entire year. Yet, depending on the stage of the cycle of rice production, similarities among waterbird communities of rice fields and those from other habitats vary significantly. The central position of rice fields likely means that they share a number of characteristics with all other habitats studied, leading to a rich waterbird community in the habitat mosaic, attracting species with very different habitat requisites such as birds that prefer areas with more permanent water bodies and also those who prefer agricultural systems.

Gradients driving the differences in waterbird communities between rice fields and other habitats

Rice fields hold a central position in the gradients described by the NMDS analyses because they present characteristics of both aquatic and terrestrial environments. Indeed, rice fields are very seasonal habitats due to the management actions related to rice farming that create drastic environmental changes over the year. This management ensures that, during spring and summer, all fields are flooded and have rice growing, providing abundant resources for aquatic predators and generalists that seek aquatic food sources. During autumn and winter, the water is drained from the paddies, and fields are harvested and ploughed. Soil mobilization leads to an instantaneous increase in food availability by destroying shelter of potential prey and scattering leftover rice. This reflects in drastic changes in the waterbird community of rice fields over the cycle of rice production, with a more generalist community with higher trophic level and larger mass during the spring/summer and a more herbivorous community with lower mass in the autumn/winter.

Lakes and saltpans remain flooded all year with some minor reduction in water volume during summer, while intertidal areas are submersed and immersed daily, according to the tide cycle. Thus, the environmental conditions in artificial lakes, saltpans and intertidal areas are mostly stable year-round. This likely links to relatively lower variability in food availability all year long compared with rice fields and pastures. Together with the permanent presence of water, these habitats attract more birds typically associated with aquatic environments and food sources.

Pastures are on another extreme of the gradient, being mostly dry year-round. Although periods of heavy rainfall may lead to short periods of flooding (few weeks), during most years pastures never get flooded and are probably less attractive for birds that prefer to forage in wet areas, namely for those seeking aquatic food items. Hence, the pastures are the most well-separated habitat in both the compositional and functional ordinations representing the habitat with the least richness and density of waterbirds in the study area.

## Species composition in rice fields and surrounding habitats across the year

The most abundant waterbird species found in rice fields are the black-tailed godwit, glossy ibis, greater flamingo and northern shoveler, while almost all white storks were counted in this habitat. All these species have been increasing their numbers in the Tagus Estuary in the last decades namely during the winter (Encarnação, 2015, 2019; Alonso et al., 2022; Martins et al., 2022). Increases in the numbers of white stork and glossy ibis have been partly attributed to the abundance of food provided by rice fields (Gilbert et al., 2015; Encarnação, 2019). During the entire period that paddies are flooded and for some time after harvesting, i.e. from April to November, rice fields provide a valuable prey for these and many other species due to the high abundance of an invasive crustacean, the Louisiana red-swamp crayfish, *Procambarus clarkii* (Girard, 1852) (Correia, 2001). In the Tagus rice fields, the diet of white storks and glossy ibis is dominated by crayfish (Ferreira et al., 2019; Andrés, 2022), but herons, egrets and gulls also consume crayfish regularly (pers. obs.). Another abundant food source in the paddies, rice, is also consumed by several species: flamingos eat newly sown seeds in spring (Tourenq et al., 2001), black-tailed godwits consume rice leftovers after harvest, i.e. mostly between November and February (Lourenço et al., 2010) and glossy ibis take both rice kernels directly from the plants (in summer) and leftovers after harvest (in autumn/winter; Toral et al., 2012; pers. obs.). Rice fields also hold a great diversity of other prey for waterbirds during the months of rice production (April to September), namely aquatic arthropods (Picazo et al., 2010) and aquatic vertebrates such as fish (Clavero et al., 2015) and amphibians (González-Solís et al., 1996). Therefore, rice fields are a very important foraging habitat for a great number of waterbirds over all stages of the rice cycle.

Lakes are dominated by duck species, namely Eurasian teal, one of the most abundant waterbird species wintering in the Tagus estuary (Moreira, 1999; Alonso et al., 2022). During the day, many duck species mostly rest in lakes, ponds, or other wetlands. After sunset, they usually move to agricultural areas, including rice fields, grassland and marshes around the resting sites, and forage on grains, weeds and invertebrates during most of nighttime (Euliss and

Harris, 1987; McNeill et al., 1992; Elphick and Oring, 1998; Guillemain et al., 2000; pers. obs.). Thus, rice fields can offer ducks foraging opportunities almost year-round and, after harvesting, from October to April, the few paddies that have been ploughed and are either flooded or wet, due to management actions or rainfall also provide resting habitat. Hence, the suitability of rice fields for ducks during most winter and spring is less predictable when compared with lakes, which can offer stable environmental conditions year-round. Yet, it is important to note that daytime resting areas, such as lakes, and nocturnal foraging areas, such as rice fields, together comprise a “functional unit” for ducks (Tamisier, 1978). The absence of one of those areas may compromise the functional unit and decreases the suitability of the entire landscape as a wintering area for ducks (Tajiri & Ohkawara, 2013). Lakes are also used as high-tide roosts by several other waterbirds (Lourenço et al., 2018), particularly shorebirds and some other duck species that feed in the intertidal areas at low tide (Recher & Recher, 1966; Moreira, 1999; Granadeiro et al., 2004; Catry et al., 2011). This explains the fact that this habitat presented the highest number of species during the entire year. Given the context of high-tide roost declines over the last decade (Catry et al., 2011; Alves et al., 2012), these lakes play a crucial role for many waterbird species preventing further declines.

Saltpans are dominated by greater flamingo for part of the year, but during most of the winter they are overtaken by large numbers of northern shoveler. The Tagus estuary has great importance for the wintering populations of northern shoveler in Europe (Moreira, 1995). Likewise, estimates from counts in the Tagus estuary indicate that flamingos account for almost 7% of the total waterbird abundance, over 10,000 individuals, using the area during the winter (Martins et al., 2022), and a smaller, yet significant, number stay all year long (Alves et al., 2012). Saltpans, like lakes, often gather large numbers of shorebirds during high-tides and for that reason have a remarkable importance for several species, offering a good quality roosting habitat (Catry et al., 2011; Alves et al., 2012). In fact, they are part of the functional unit formed by lakes, saltpans and rice fields for night foragers such as ducks and flamingos (Tamisier, 1978) that rest in saltpans and lakes during the day and forage in rice fields during the night.

The intertidal areas are dominated by waders, and the value of this habitat as foraging ground for wintering and stopping-over birds is undisputed (Recher & Recher, 1966; Moreira, 1999; Granadeiro et al., 2004; Catry et al., 2011). In comparison, rice fields are of lesser importance, except for black-tailed godwit (Lourenço et al., 2010). Therefore, this work suggests that rice fields alone cannot compensate for the potential loss of intertidal areas for waders.

Contrary to all other habitats, the pastures have relatively low numbers for most waterbirds being dominated by a generalist species, heavily associated with agricultural systems, the cattle egret (Talbi et al., 2023). Although white stork is one of the most abundant waterbird species in pastures, stork abundance and density in rice fields are tenfold higher.

#### Functional structure of waterbird communities in rice fields and surrounding habitats across the year

From April to September, the waterbird community of rice fields seems to be characterized mainly by large species, with proportionally long wings, high trophic level and a generalist diet. Some of these species (often classified as vertebrate predators), such as storks, gulls, herons and egrets, are actually targeting a particular invertebrate pest in the rice fields of the Tagus River, the Louisiana red-swamp crayfish, *Procambarus clarkii* (Correia, 2001). The relatively large size and high abundance of crayfish make them particularly attractive for large and medium avian predators, likely explaining the dominance of these traits among the waterbird community using rice fields.

From December to February, the waterbird community in rice fields changes towards a dominance of smaller, herbivorous birds with wider beaks, mostly ducks. This is linked to the arrival of many migratory duck species that are attracted to rice paddies with high availability of rice leftovers (Lourenço et al., 2010), earthworms (Lourenço & Piersma, 2008), algae and macrophytes (Martínez-Eixarch et al., 2017).

Lakes are also dominated by herbivores with wide beaks, and these results mirror the results obtained from the community structure, since these traits are associated with ducks and their year-round abundance in lakes.

Greater flamingo and northern shoveler are key species in saltpans for most of the winter. Both

species are large migratory aquatic predators which explains the dominance of these traits in saltpans. Yet, in the context of rice production, flamingos are viewed as a pest, being one of the most problematic species worldwide in terms of perceived damage to rice fields (Johnson & Mesléard, 1997; Moreno-Opo & Piqué, 2018). They gather around rice fields after sowing, killing the seeds through suffocation due to trampling and to the increased turbidity of the water, while also directly consuming the seeds (Tourenq et al., 2001; Ernoul et al., 2013). Across Europe, the losses in rice production attributed to flamingos can range from 5 to 10% (Johnson & Mesléard, 1997). The proximity between saltpans and rice fields in the Tagus estuary facilitates their presence and potential damages.

The intertidal areas are dominated by waterbirds with high hand-wing index, typical of migratory species. Larger values of this index indicate longer, more pointed wings, which are positively correlated with greater flight efficiency (reduced drag, increased lift) and higher speed (less air resistance; Lockwood et al., 1998). Thus, it is usually higher in birds that exhibit migratory behaviour (Sheard et al., 2022). Rice fields are also used by many migratory species such as black-tailed godwit, but overall, the importance of intertidal areas for migratory species seems to be higher, as indicated by the higher CWM of hand-wing index. This, again, suggests that the loss of intertidal areas, may not be mitigated by the presence of rice fields, particularly for migratory species.

#### Ecosystem functions and services of waterbird communities in rice fields and surrounding habitats

The functional structure of the waterbird community using rice fields over the year links to many important ecosystem functions and services, some of which directly benefiting the production of rice. Since there are changes in this functional structure over the year, the relative importance of different functions and services also changes.

The body mass of waterbirds strongly relates to a range of other traits including metabolic rate, foraging behaviour, longevity and home-range size (Luck et al., 2012), which are particularly important given the high mass of the birds using rice fields. Larger animals mobilize a higher amount of nutrients, disproportionately contributing to nutrient cycling

(Elser & Urabe, 1999; Brown et al., 2004). Also, larger animals have a higher secondary production, namely if they are predators (Woodward et al., 2005b), as is the case of most waterbirds in rice fields. These characteristics make them an important source of fertilization for the soil, increasing soil health and reducing artificial fertilizer requirements, thus, also reducing the cost of rice production (Firth et al., 2020). Moreover, larger birds tend to live longer (Woodward et al., 2005a; Luck et al., 2012) and to have larger home-ranges (Woodward et al., 2005a), meaning that their functions and services likely spread to adjacent habitats. Finally, larger birds also play a role in cultural services, namely in birdwatching, often being recognized as a symbol of the Tagus estuary and neighbouring rice fields.

The dominance of predators among the waterbirds using rice fields during the rice growing period also speak for their value as pest control (Whelan et al., 2008), particularly because they target crayfish as their main prey (Correia, 2001). Crayfish negatively affect rice production (Lodge & Lorma, 1987; Lodge, 1991; Lodge et al., 1994; Momot, 1995; Nyström & Strand, 1996; Anastácio & Marques, 1997), and so the presence of birds during the rice cultivation period is extremely valuable.

From December to February, herbivore traits dominate in rice fields. Herbivores are primary consumers, contributing to nutrient cycling, stimulating primary productivity, and increasing plant diversity (Green & Elmerg, 2014), and providing fertilization for the soil with droppings and transport plant propagules (Buij et al., 2017). For a short period of the year, the waterbirds using rice fields seem to be able to provision these ecosystem services and functions. Herbivores can also help control weeds (Green & Elmerg, 2014), although this service may be more important during the rice growing period (April to September).

The functional structure of the waterbird community in lakes is similar to the one recorded in rice fields from December to February. Contrary to rice fields, however, these traits seem to be prevalent in lakes for the entire year. Hence, the importance of waterbirds in lakes for some ecosystem functions and services related with herbivory, namely those not related with foraging (since the lakes are mostly used as roosting habitat), is much more exacerbated

(Green & Elmerg, 2014) and probably far surpasses the ability of rice fields to provide them.

Saltpans are dominated by large aquatic predators, including flamingos, that play an important role in nutrient cycling (Elser & Urabe, 1999; Brown et al., 2004), and their foraging strategy generates bioturbation as they move (Lee & Mayorga-Dussarrat, 2016), contributing to the acceleration of the decomposition processes (Van Groenigen et al., 2003). Yet, since most waterbirds are not using saltpans to forage, the impact of these functions and services may be felt with more intensity in foraging habitats, such as rice fields and intertidal areas.

Intertidal areas support several waterbird species with long distance migratory behaviour, some of which may cross three continents every year (Catry et al., 2016). Thus, birds in these areas are sensitive to any changes in landscape connectivity and food availability that may occur along their entire migratory routes (Luck et al., 2012). Therefore, as suggested by previous studies (Piersma & Lindström, 2004), waterbirds using intertidal areas can act as sentinel species, detecting not only local environmental changes but also global ones, to a degree unmatched by any other studied community, including that using rice fields. Intertidal areas are particularly important from an international standpoint since the waterbirds using intertidal areas, and the functions and services they perform, such as regulating the abundance of their prey community, regulating sediment–water nutrient fluxes in the mudflat and preventing its erosion (Booty et al., 2020), affect not only the study area but also areas of the world far beyond the Tagus estuary, along all the East Atlantic Flyway (Catry et al., 2016).

The high overlap between intertidal areas and saltpans in the functional structure ordination may indicate that the most abundant functional groups that feed in the intertidal areas also use saltpans, probably as a resting habitat. As such, some ecosystem functions and services performed by the waterbirds using these habitats may be redundant, but the distinction between intertidal areas and saltpans as foraging vs. resting grounds also indicates a strong complementarity between them, indicating that the loss of one could compromise the functioning and services of the other.

To conclude, this work brings important arguments to the discussion on whether rice fields can compensate for the loss of natural wetlands, providing

high-quality habitat for waterbird communities. Our results indicate that rice fields support a waterbird community with distinct composition and functional structure from those of the remaining habitats over the entire year, suggesting they play a role as complementary habitats in the mosaic landscape, not redundant. Rice fields may play a similar role as an ecotone, a zone of transition between adjacent ecological systems (Holland, 1988), by displaying characteristics from both wetlands and agricultural lands, hence allowing for the coexistence of species with preferences for each habitat type. Moreover, since waterbirds often commute among habitats (pers. obs.), namely between foraging habitats (intertidal areas and rice fields) and roosting habitats (saltpans and lakes), rice fields may act as a central node for waterbirds using the landscape mosaic. Yet, rice fields are not the richest habitat in the study area in terms of waterbirds, suggesting that the loss of the remaining habitats cannot be fully compensated by the presence of rice fields. Given the present context of worldwide wetland loss (Ballut-Dajud et al., 2022; Fluet-Chouinard et al., 2023), rice fields can act as a buffer habitat, whose presence minimizes the potential loss of at least some waterbird species. It should be emphasized that while rice cultivation is a monospecific homogeneous habitat, it supports a waterbird community performing important ecosystem functions and services that benefits both natural processes and the rice production industry. These benefits and the conservation potential of rice fields for waterbirds can be further enhanced by implementing agri-environmental schemes (Chang et al., 2017), such as managing flood timing to provide quality habitat outside the rice growing season (Golet et al., 2018) and breeding areas for birds during the rice growing season (Herring et al., 2021). Thus, despite being an artificial habitat, rice fields are likely one of the most valuable agricultural systems for waterbird biodiversity.

**Acknowledgements** We thank Associação de Beneficiários da Lezíria Grande de Vila Franca de Xira (ABLGVSX), namely Rui Paixão and Fortunato Pereira, and Espaço de Visitação e Observação de Aves (EVOA), namely Sandra Silva and Andreia Silva, for the permissions and critical logistic support to work on the field. Beatriz Andréis provided help in various phases of the fieldwork.

**Author contributions** JP, JPG and TC contributed to the study conception and design. Material preparation and data collection were performed by JP. All authors contributed to the

data analysis. The first draft of the manuscript was written by JP and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Funding** Open access funding provided by FCTIFCCN (b-on). This work was supported by Fundação para a Ciência e Tecnologia (FCT) and Ministério da Ciência, Tecnologia e Ensino Superior (MCTES) with financial support to CESAM (<https://doi.org/10.54499/UIBP/50017/2020> + <https://doi.org/10.54499/UIDB/50017/2020> + <https://doi.org/10.54499/LA/P/0094/2020>), through national funds. JP and PM were also supported by FCT through a doctoral grant (<https://doi.org/10.54499/2020.07656.BD>) and contract (2020.03347.CEECIND), respectively.

**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interests** The authors have no relevant financial or non-financial interests to disclose.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

#### References

- Alonso, H., J. Andrade, J. Teodósio, & A. Lopes, 2022. O estado das aves em Portugal, 2022. Lisbon.
- Alves, J. A., P. M. Lourenço, M. P. Dias, A. Antunes, T. Catry, H. Costa, P. Fernandes, B. Ginja, J. Jara, R. Martins, F. Moniz, S. Pardal, T. Pereira, M. J. Rainho, A. Rocha, J. C. Rodrigues & M. Rolo, 2012. Monitoring waterbird populations on the Tejo, Sado and Guadiana estuaries, Portugal: 2011 report. *Anuário Ornitológico* 9: 66–87.
- Anastácio, P. M. & J. C. Marques, 1997. Crayfish, *Procambarus clarkii*, effects on initial stages of rice growth in the lower Mondego River valley (Portugal). *Freshwater Crayfish* 11: 608–617.
- Andrés, B., 2022. Utilização dos arrozais do estuário do Tejo por Íbis-preta e Cegonha-branca: ecologia alimentar e conflitos na produção de arroz. Master thesis, Faculty of Sciences of the University of Lisbon.

- Ballut-Dajud, G. A., L. C. S. Herazo, G. Fernández-Lambert, J. L. Marín-Muñiz, M. C. L. Méndez & E. A. Betanzo-Torres, 2022. Factors affecting wetland loss: a review. *Land* 11: 434.
- Booty, J. M., G. J. C. Underwood, A. Parris, R. G. Davies & T. J. Tolhurst, 2020. Shorebirds affect ecosystem functioning on an intertidal mudflat. *Frontiers in Marine Science* 7: 1–15.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage & G. B. West, 2004. Toward a metabolic theory of ecology. *Ecological Society of America* 85: 1771–1789.
- Buij, R., T. C. P. Melman, M. J. J. E. Loonen & A. D. Fox, 2017. Balancing ecosystem function, services and disservices resulting from expanding goose populations. *Ambio* 46: 301–318.
- Catry, T., J. A. Alves, J. Andrade, H. Costa, M. P. Dias, P. Fernandes, A. Leal, P. M. Lourenço, R. C. Martins, F. Moniz, S. Pardal, A. Rocha, C. D. Santos, V. Encarnaçao & J. P. Granadeiro, 2011. Long-term declines of wader populations at the Tagus estuary, Portugal: a response to global or local factors? *Bird Conservation International* 21: 438–453.
- Catry, T., P. M. Lourenço, R. J. Lopes, C. Carneiro, J. A. Alves, J. Costa, H. Rguibi-Idrissi, S. Bearhop, T. Piersma & J. P. Granadeiro, 2016. Structure and functioning of intertidal food webs along an avian flyway: a comparative approach using stable isotopes. *Functional Ecology* 30: 468–478.
- Chang, S.-H.-E., D. Wuepper, A. Heissenhuber & J. Sauer, 2017. Investigating rice farmers' preferences for an agri-environmental scheme: Is an eco-label a substitute for payments? *Land Use Policy* 64: 374–382.
- Clavero, M., V. López, N. Franch, Q. Pou-Rovira & J. M. Queral, 2015. Use of seasonally flooded rice fields by fish and crayfish in a Mediterranean wetland. *Agriculture, Ecosystems and Environment* 213: 39–46.
- Coelho, M. C. M., R. Gabriel, H. Hespagnol, P. A. V. Borges & C. Ah-Peng, 2021. Bryophyte diversity along an elevational gradient on Pico island (Azores, Portugal). *Diversity* 13: 1–32.
- Cornwell, W. K. & D. D. Ackerly, 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- Correia, A. M., 2001. Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *Journal of Zoology* 255: 533–541.
- Delany, S., D. Scott, T. Dodman & D. Stroud, 2009. An Atlas of Wader Populations in Africa and Western Eurasia. Wetlands International and International Wader Study Group, Wageningen.
- Díaz, S. & M. Cabido, 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646–655.
- Díaz, S., S. Lavorel, F. De Bello, F. Quétier, K. Grigulis & T. M. Robson, 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America* 104: 20684–20689.
- Dormann, C. F., B. Gruber & J. Fruend, 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8: 8–11.
- Elphick, C. S., 2000. Functional equivalency between rice fields and seminatural wetland habitats. *Conservation Biology* 14: 181–191.
- Elphick, C. S., 2015. A history of ecological studies of birds in rice fields. *Journal of Ornithology* 156: 239–245.
- Elphick, C. S. & L. W. Oring, 1998. Winter management of Californian rice fields for waterbirds. *Journal of Applied Ecology* 35: 95–108.
- Elphick, A., S. Chris & C. Katharine, 2010. The future for research on waterbirds in rice fields. *Waterbirds* 33: 231–243.
- Elser, J. J. & J. Urabe, 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* 80: 735–751.
- Encarnaçao, V., 2015. Relatório do VI Censo Nacional de Cegonha-branca *Ciconia ciconia*—2014. Lisbon.
- Encarnaçao, V., 2019. Status of the Glossy ibis *Plegadis falcinellus* breeding and wintering in Portugal. *SIS Conservation* 1: 78–81.
- Ernoul, L., F. Mesléard, P. Gaubert & A. Béchet, 2013. Limits to agri-environmental schemes uptake to mitigate human-wildlife conflict: lessons learned from Flamingos in the Camargue, southern France. *International Journal of Agricultural Sustainability* 12: 23–36.
- Euliss, N. H. & S. W. Harris, 1987. Feeding ecology of northern pintails and green-winged teal wintering in California. *The Journal of Wildlife Management* 51: 724–732.
- Fasola, M. & X. Ruiz, 1996. The value of rice fields as substitutes for natural wetlands for waterbirds in the Mediterranean Region. *Waterbirds* 19: 122–128.
- Ferreira, E., F. Grilo, R. Mendes, R. Lourenço, S. Santos & F. Petrucci-Fonseca, 2019. Diet of the White Stork (*Ciconia ciconia*) in a heterogeneous Mediterranean landscape: the importance of the invasive Red Swamp Crayfish (*Procambarus clarkii*). *Airo* 26: 33–47.
- Firth, A. G., B. H. Baker, J. P. Brooks, R. Smith, R. B. Iglay & J. Brian Davis, 2020. Low external input sustainable agriculture: winter flooding in rice fields increases bird use, fecal matter and soil health, reducing fertilizer requirements. *Agriculture, Ecosystems and Environment* 300: 106962.
- Fluet-Chouinard, E., B. D. Stocker, Z. Zhang, A. Malhotra, J. R. Melton, B. Poulter, J. O. Kaplan, K. K. Goldewijk, S. Siebert, T. Minayeva, G. Hugelius, H. Joosten, A. Barthelme, C. Prigent, F. Aires, A. M. Hoyt, N. Davidson, C. M. Finlayson, B. Lehner, R. B. Jackson & P. B. McIntyre, 2023. Extensive global wetland loss over the past three centuries. *Nature* 614: 281–286.
- Garnier, E., J. Cortez, G. Billès, M. L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill & J. P. Toussaint, 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.
- Gilbert, N. I., R. A. Correia, J. P. Silva, C. Pacheco, I. Catry, P. W. Atkinson, J. A. Gill & A. M. Aldina, 2015. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks

- (*Ciconia ciconia*) from a partially migratory population. *Movement Ecology* 4: 7.
- Golet, G. H., C. Low, S. Avery, K. Andrews, C. J. McColl, R. Laney & M. D. Reynolds, 2018. Using ricelands to provide temporary shorebird habitat during migration. *Ecological Applications* 28: 409–426.
- González-Solís, J., X. Bernardí & X. Ruiz, 1996. Seasonal variation of waterbird prey in the ebro delta rice fields. *Colonial Waterbirds* 19: 135–142.
- Granadeiro, J. P., J. Andrade & J. M. Palmeirim, 2004. Modelling the distribution of shorebirds in estuarine areas using generalised additive models. *Journal of Sea Research* 52: 227–240.
- Green, A. J. & J. Elmberg, 2014. Ecosystem services provided by waterbirds. *Biological Reviews* 89: 105–122.
- Guillemain, M., H. Fritz & S. Blais, 2000. Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*). *Behavioural Processes* 50: 123–129.
- Henriques, J. F., P. C. Tavares, M. M. Correia-Dos-Santos, M. A. Trancoso, M. Santos-Reis & C. Branquinho, 2014. Monitoring Hg and Cd contamination using red swamp crayfish (*Procambarus clarkii*): implications for wetland food chain contamination. *Water, Air, and Soil Pollution* 225: 2210.
- Herring, M. W., W. A. Robinson, K. K. Zander & S. T. Garnett, 2021. Increasing water-use efficiency in rice fields threatens an endangered waterbird. *Agriculture, Ecosystems and Environment* 322: 107638.
- Hevia, V., B. Martín-López, S. Palomo, M. García-Llorente, F. de Bello & J. A. González, 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: synthesizing existing evidence and future challenges. *Ecology and Evolution* 7: 831–844.
- Holland, M. M., 1988. SCOPE/MAB Technical consultations on landscape boundaries. Report of a SCOPE/MAB workshop on ecotones. In di Castri, F., A. J. Hansen & M. M. Holland (eds), *A New Look at Ecotones: Emerging International Projects on Landscape Boundaries* Biology International, Paris: 47–106.
- Hooper, D. U., F. S. Chapin III., J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmidt, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monography* 75: 3–35. <https://doi.org/10.1890/04-0922>.
- Iken, F., 2017. Na lezíria ribatejana, com um emblemático arroz: As malandricas do carolino. *Revista de Vinhos: A Essência do Vinho Porto* 1–5, <https://www.revistadevinhos.pt/comer/na-leziria-ribatejana-com-um-emblematico-arroz>.
- International Rice Research Institute, 1995. *World Rice Statistics 1993–94*. IRRI, Los Baños.
- Johnson, A. R., & F. Mesléard, 1997. Oiseaux à Risques en Ville et à la Campagne In Clergeau, P. (ed), *Les flamants et la riziculture*. INRA Editions, Paris: 53–60.
- Katayama, N., Y. Odaya, T. Amano & H. Yoshida, 2020. Spatial and temporal associations between fallow fields and Greater Painted Snipe density in Japanese rice paddy landscapes. *Agriculture, Ecosystems and Environment* 295: 106892.
- Kraft, N. J. B., O. Godoy & J. M. Levine, 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America* 112: 797–802.
- Laliberte, E. & P. Legendre, 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Laliberté, E., & P. Legendre, 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. R CRAN package, Vienna.
- Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrrough, S. Berman, F. Quéfier, A. Thébault & A. Bonis, 2008. Assessing functional diversity in the field—methodology matters! *Functional Ecology* 22: 134–147.
- Lee, M. R. & J. Mayorga-Dussarrat, 2016. The impact of feeding by Chilean flamingos (*Phoenicopterus chilensis*) on the meiofaunal assemblage of a tidal flat. *Marine Biology Research* 12: 1039–1052.
- Legendre, P. & L. Legendre, 2012. Ordination in reduced space. *Developments in Environmental Modelling* 24: 425–520.
- Leitão, S., P. Pinto, T. Pereira & M. F. Brito, 2007. Spatial and temporal variability of macroinvertebrate communities in two farmed Mediterranean rice fields. *Aquatic Ecology* 41: 373–386.
- Lockwood, R., J. P. Swaddle & J. M. V. Rayner, 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29: 273–292.
- Lodge, D. M., 1991. Herbivory on freshwater macrophytes. *Aquatic Botany* 41: 195–224.
- Lodge, D. M. & J. G. Lorma, 1987. Reductions in submersed macrophyte biomass and species richness by the Crayfish *Orconectes rusticus*. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 591–597.
- Lodge, D. M., M. W. Kershner, J. E. Aloï & A. P. Covich, 1994. Effects of an omnivorous Crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75: 1265–1281.
- Lourenço, P. M. & T. Piersma, 2008. Stopover ecology of Black-tailed Godwits *Limosa limosa limosa* in Portuguese rice fields: a guide on where to feed in winter. *Bird Study* 55: 194–202.
- Lourenço, P. M. & T. Piersma, 2009. Waterbird densities in South European rice fields as a function of rice management. *Ibis* 151: 196–199.
- Lourenço, P. M., F. S. Mandema, J. C. E. W. Hooijmeijer, J. P. Granadeiro & T. Piersma, 2010. Site selection and resource depletion in black-tailed godwits *Limosa l. limosa* eating rice during northward migration. *Journal of Animal Ecology* 79: 522–528.
- Lourenço, P. M., H. Alonso, J. A. Alves, A. T. Carvalho, T. Catry, H. Costa, J. S. Costa, M. P. Dias, P. Fernandes, A. I. Leal, R. C. Martins, F. Moniz, S. Pardal & C. D. Santos, 2018. Monitoring waterbird populations in the Tejo estuary, Portugal: report for the decade 2007–2016. *Airo* 25: 3–31.

- Luck, G. W., S. Lavorel, S. McIntyre & K. Lumb, 2012. Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology* 81: 1065–1076.
- Martínez-Eixarch, M., A. Curcó & C. Ibáñez, 2017. Effects of agri-environmental and organic rice farming on yield and macrophyte community in Mediterranean paddy fields. *Paddy and Water Environment* 15: 457–468.
- Martins, R. C., F. Moniz, J. A. Alves, J. Belo, A. T. Carvalho, T. Catry, A. Cordeiro, H. Costa, J. S. Costa, V. Encarnação, P. M. Lourenço, J. Nightingale, S. Pardal, J. Paulino, D. Raposo, A. Rocha, A. Silvério, & M. P. Dias, 2022. Contagens Mensais de Aves Aquáticas no Estuário do Tejo, 2007–2021 In Alonso, H., J. Andrade, J. Teodósio, & A. Lopes (eds), *O estado das aves em Portugal, 2022*. Sociedade Portuguesa para o Estudo das Aves, Lisbon: 65–69.
- McCune, B., J. B. Grace & D. L. Urban, 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach.
- McNeill, R., P. Drapeau & J. D. Goss-Custard, 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Reviews* 67: 381–419.
- Mitsch, W. J. & J. G. Gosselink, 2000. *Wetlands*, 3rd ed. Van Nostrand, New York.
- Mitsch, W. J. & Ü. Mander, 2018. Wetlands and carbon revisited. *Ecological Engineering* 114: 1–6. <https://doi.org/10.1016/j.ecoleng.2017.12.027>.
- Momot, W. T., 1995. Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3: 33–63.
- Moreira, F., 1995. A utilização das zonas entre-marés do estuário do Tejo por aves aquáticas e suas implicações para os fluxos de energia na teia trófica estuarina. PhD Thesis, Faculty of Sciences, University of Lisbon.
- Moreira, F., 1999. On the use by birds of intertidal areas of the Tagus estuary: implications for management. *Aquatic Ecology* 33: 301–309.
- Moreno-Opo, R. & J. Piqué, 2018. Reconciling the conservation of the purple swamphen (*Porphyrion porphyrio*) and its damage in Mediterranean rice fields through sustainable non-lethal techniques. *PeerJ* 6: e4518.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason & D. R. Bellwood, 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28: 167–177.
- Naeem, S. & J. P. Wright, 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6: 567–579.
- Nelson, A., T. Setiyono, A. B. Rala, E. D. Quicho, J. V. Raviz, P. J. Abonete, A. A. Maunahan, C. A. Garcia, H. Z. M. Bhatti, L. S. Villano, P. Thongbai, F. Holecz, M. Barbieri, F. Collivignarelli, L. Gatti, E. J. P. Quilang, M. R. O. Mabalay, P. E. Mabalot, M. I. Barroga, A. P. Bacong, N. T. Detoito, G. B. Berja, F. Varquez, D. Wahyunto, S. R. Kuntjoro, S. Murdiyati, P. Pazhanivelan, P. C. Kannan, E. Nirmala Mary, P. Subramanian, A. Rakwatin, T. Intrman, S. Setapayak, V. Q. Lertna, V. Q. Minh, T. H. Tuan, N. H. Duong, D. Van. Quyen, S. Kham, T. Hin, M. Veasna, C. Chin. Yadav & N. H. Ninh, 2014. Towards an operational SAR-based rice monitoring system in Asia: examples from 13 demonstration sites across Asia in the RIICE project. *Remote Sensing* 6: 10773–10812.
- Nyström, P. & J. A. Strand, 1996. Grazing by a native and an exotic crayfish on aquatic macrophytes. *Freshwater Biology* 36: 673–682.
- Okasen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2013. *vegan: Community Ecology Package*. R CRAN package, Vienna.
- Parejo, M., J. S. Gutiérrez, J. G. Navedo, A. Soriano-Redondo, J. M. Abad-Gómez, A. Villegas, C. Corbacho, J. M. Sánchez-Guzmán & J. A. Masero, 2019. Day and night use of habitats by northern pintails during winter in a primary rice-growing region of Iberia. *PLoS ONE* 14: 1–16.
- Parsons, K. & P. Mineau, 2010. Effects of pesticide use in rice fields on birds. *Waterbirds* 33: 193–218.
- Picazo, F., J. L. Moreno & A. Millán, 2010. The contribution of standing waters to aquatic biodiversity: the case of water beetles in southeastern Iberia. *Aquatic Ecology* 44: 205–216.
- Pierluissi, S., 2010. Breeding waterbirds in rice fields: a global review. *Waterbirds* 33: 123–132.
- Piersma, T. & Å. Lindström, 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis* 146: 61–69.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Ramsar Convention Secretariat, 2010. *Wetland inventory: A Ramsar framework for wetland inventory and ecological character description*. Ramsar Convention Secretariat, Gland.
- Recher, H. F. & J. A. Recher, 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47: 393–407.
- Ribeiro, J., G. R. Colli & A. Soares, 2019. Landscape correlates of anuran functional connectivity in rice crops: a graph-theoretic approach. *Journal of Tropical Ecology* 35: 118–131.
- Seck, P. A., A. Diagne, S. Mohanty & M. C. S. Wopreis, 2012. Crops that feed the world 7: rice. *Food Security* 4: 7–24.
- Sheard, C., M. H. C. Neate-Clegg, N. Alioravainen, S. E. I. Jones, C. Vincent, H. E. A. Macgregor, T. P. Bregman, S. Claramunt & J. A. Tobias, 2022. The latitudinal gradient in hand-wing-index: global patterns and predictors of wing morphology in birds. *Biological Journal of the Linnean Society* 137: 137–144. <https://doi.org/10.1101/816603>.
- Sonnier, G., B. Shipley & M. L. Navas, 2010. Quantifying relationships between traits and explicitly measured gradients of stress and disturbance in early successional plant communities. *Journal of Vegetation Science* 21: 1014–1024.
- Tajiri, H. & K. Ohkawara, 2013. The effects of flooding and plowing on foraging site selection by wintering dabbling ducks in rice fields. *Ornithological Science* 12: 127–136.
- Talbi, R., Y. Gavish, I. Izhaki & A. Bar-Massada, 2023. When a pest-control species becomes a pest: a shift in the foraging habitat of cattle egret (*Bubulcus ibis*) and the threat to grazed natural ecosystems. *Biological Conservation* 282: 110067.

- Tamisier, A., 1978. The functional units of wintering ducks: a spatial integration of their comfort and feeding requirements. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* 23: 229–238.
- Tobias, J. A., C. Sheard, A. L. Pigot, A. J. M. Devenish, J. Yang, F. Sayol, M. H. C. Neate-Clegg, N. Alioravainen, T. L. Weeks, R. A. Barber, P. A. Walkden, H. E. A. MacGregor, S. E. I. Jones, C. Vincent, A. G. Phillips, N. M. Marples, F. A. Montaña-Centellas, V. Leandro-Silva, S. Claramunt, B. Darski, B. G. Freeman, T. P. Bregman, C. R. Cooney, E. C. Hughes, E. J. R. Capp, Z. K. Varley, N. R. Friedman, H. Korntheuer, A. Corrales-Vargas, C. H. Trisos, B. C. Weeks, D. M. Hanz, T. Töpfer, G. A. Bravo, V. Remeš, L. Nowak, L. S. Carneiro, A. J. R. Moncada, B. Matysioková, D. T. Baldassarre, A. Martínez-Salinas, J. D. Wolfe, P. M. Chapman, B. G. Daly, M. C. Sorensen, A. Neu, M. A. Ford, R. J. Mayhew, L. Fabio Silveira, D. J. Kelly, N. N. D. Annorbah, H. S. Pollock, A. M. Grabowska-Zhang, J. P. McEntee, J. Carlos, T. Gonzalez, C. G. Meneses, M. C. Muñoz, L. L. Powell, G. A. Jamie, T. J. Matthews, O. Johnson, G. R. R. Brito, K. Zyskowski, R. Crates, M. G. Harvey, M. Jurado Zevallos, P. A. Hosner, T. Bradfer-Lawrence, J. M. Maley, F. G. Stiles, H. S. Lima, K. L. Provost, M. Chibesa, M. Mashao, J. T. Howard, E. Mlamba, M. A. H. Chua, B. Li, M. I. Gómez, N. C. García, M. Päckert, J. Fuchs, J. R. Ali, E. P. Derryberry, M. L. Carlson, R. C. Urriza, K. E. Brzeski, D. M. Prawiradilaga, M. J. Rayner, E. T. Miller, R. C. K. Bowie, R. M. Lafontaine, R. P. Scofield, Y. Lou, L. Somarathna, D. Lepage, M. Illif, E. L. Neuschulz, M. Templin, D. M. Dehling, J. C. Cooper, O. S. G. Pauwels, K. Analuddin, J. Fjeldså, N. Seddon, P. R. Sweet, F. A. J. DeClerck, L. N. Naka, J. D. Brawn, A. Aleixo, K. Böhnig-Gaese, C. Rahbek, S. A. Fritz, G. H. Thomas & M. Schleuning, 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* 25: 581–597.
- Toral, G. M., R. A. Stillman, S. Santoro & J. Figuerola, 2012. The importance of rice fields for glossy ibis (*Plegadis falcinellus*): management recommendations derived from an individual-based model. *Biological Conservation* 148: 19–27.
- Tourenq, C., S. Aulagnier, L. Durieux, S. Lek, F. Mesléard, A. Johnson & J. L. Martin, 2001. Identifying rice fields at risk from damage by the greater flamingo. *Journal of Applied Ecology* 38: 170–179.
- Van Groenigen, J. W., E. G. Burns, J. M. Eadie, W. R. Horwath & C. Van Kessel, 2003. Effects of foraging waterfowl in winter flooded rice fields on weed stress and residue decomposition. *Agriculture, Ecosystems and Environment* 95: 289–296.
- Whelan, C. J., D. G. Wenny & R. J. Marquis, 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences* 1134: 25–60.
- Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. Rivadeneira & W. Jetz, 2016. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95: 2027.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido & P. H. Warren, 2005a. Body size in ecological networks. *Trends in Ecology and Evolution* 20: 402–409.
- Woodward, G., D. C. Speirs & A. G. Hildrew, 2005b. Quantification and resolution of a complex, size-structured food web. *Advances in Ecological Research* 36: 85–131.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. U. NavasLoNinimets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas & R. Villar, 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Xu, S., X. Liu, X. Li & C. Tian, 2019. Soil organic carbon changes following wetland restoration: a global meta-analysis. *Geoderma* 353: 89–96. <https://doi.org/10.1016/j.geoderma.2019.06.027>.
- Yoon, C. G., 2009. Wise use of paddy rice fields to partially compensate for the loss of natural wetlands. *Paddy and Water Environment* 7: 357–366.

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.