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Research Article

Assessing the use of inland wetlands by fishes in the Lower Tagus Basin, Portugal

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Abstract

Although inland wetlands are among the most important and impacted biodiversity hotspots worldwide, they remain poorly assessed. This is particularly concerning in regions harboring endangered endemic species and facing strong anthropogenic pressures, such as the Lower Tagus Basin in Portugal. Here we aimed to assess the use of inland wetlands in the Lower Tagus basin by native and non-native fishes and examine the environmental factors influencing community structure. Using Sentinel-2 multispectral imagery and the Normalized Difference Water Index (NDWI), we identified 409 water surfaces, 30 of which with potential to sustain fishes over time. We surveyed 11 wetlands for fishes using a standardized, multi-gear sampling approach. We found that local fish communities were dominated by non-native species, with deep, paleopotamic wetlands (e.g., Golegã and Gouxa) tending to function as reservoirs for Largemouth Bass (*Micropterus nigricans*) and Pumpkinseed Sunfish (*Lepomis gibbosus*). Conversely, parapotamic wetlands directly connected to the Tagus River (e.g., Setil and Sto. Estevão) appeared to provide migration corridors for Thin Lip Grey Mullet (*Chelon ramada*) and shallow wetlands (e.g., Caniceiras and Granho) serve as refuges for native and threatened Lisbon Arched-mouth Nase (*Iberochondrostoma olisiponense*), European Eel (*Anguilla anguilla*), and Southern Iberian Spined Loach (*Cobitis paludica*). Our findings highlight that wetlands in the Lower Tagus Basin play different roles in supporting both native and non-native fishes. Shallow and parapotamic wetlands should be prioritized in restoration actions to hamper native fish loss whereas paleopotamic wetlands require non-native eradication and control programs to hinder the spread of non-native fishes.

Key words: Aquatic habitats, endangered fishes, freshwater biodiversity, invasive fishes, remote sensing

Introduction

Inland wetlands are declining faster than any other freshwater ecosystems in Europe and are also being lost at an alarming rate elsewhere (Malak et al. 2019). During the 20th century, 64 to 71% of wetlands present in 1900 were lost worldwide (Gardner and Finlayson 2018; Davidson 2018; Convention on Wetlands 2025). Threats to freshwater species dependent on wetlands are well documented, with numerous species listed as endangered and experiencing severe declines (Gibbs 2000; Finlayson 2012). Inland wetlands play a crucial role in meeting global commitments established under the post-2020 Global Biodiversity framework (CBD 2021) and the European Union Biodiversity Strategy 2030 (EC 2020) (Thorslund et al. 2017; Dudgeon and Strayer 2025; Convention on Wetlands 2025), and are central to restoration initiatives implemented globally to halt the decline of freshwater biodiversity (Geijzendorffer et al. 2019a; Tickner et al. 2020). However, most (89%) inland wetlands remain unprotected (Reis et al. 2017).

Information on inland wetlands remains largely incomplete (Davidson et al. 2019; Geijzendorffer et al. 2019b), despite playing critical roles, for example in supporting biodiversity, ecosystem services, and human well-being (Finlayson et al. 2005; De Groot et al. 2012; Cimon-Morin et al. 2016; Convention on Wetlands 2025). Recently, wetland assessments have benefited from remote sensing approaches, utilizing high resolution multispectral imagery, LiDAR, and Geographic Information Systems (GIS), enabling automated or semi-automated identification of wetlands (Kloiber et al. 2015; Hu et al. 2017; Lefebvre et al. 2019). Nevertheless, scarce and outdated data on wetland distribution and condition hinder biodiversity surveys and conservation and management actions.

In the Iberian Peninsula, inland wetlands have been recognized as key nurseries, feeding habitats, and refuges for freshwater fishes (Maceda-Veiga 2013). However, inland waters in this region have been extensively modified; with, for instance, drainage, river regulation, hydrological engineering, and intensive agriculture resulting in habitat fragmentation and loss of connectivity with river channels (Maceda-Veiga 2013; Fernandes et al. 2020). These alterations have likely facilitated the introduction and spread of invasive non-native species (Soto et al. 2025), but the extent to which this has affected native communities and promoted biotic homogenization remains poorly understood (Clavero and Hermoso 2011; Radinger and Garcia-Berthou 2020).

The Lower Tagus Basin in Portugal, historically characterized by a dynamic mosaic of oxbows, marshlands, and seasonally flooded habitats, is currently dominated by intensive agriculture, with some inland wetlands persisting as isolated, artificialized remnants constrained by hydrological barriers (Cordovil et al. 2018; Fernandes et al. 2020). In the last two decades, the region has been invaded by both apex predators and forage fish (Ribeiro et al. 2009; Gkenas et al. 2015; Martelo et al. 2021), whose impacts may be exacerbated in fragmented inland wetlands, where native species already face isolation and hybridization risks (Ribeiro et al. 2021; Curto et al. 2022; Latorre et al. 2023). This is of particular concern given that the Lower Tagus Basin is home to several fish species endemic to the Iberian Peninsula (Collares-Pereira et al. 2021; Magalhães et al. 2023), including the locally restricted, highly fragmented, and endangered Lisbon Arched-mouth Nase, *Iberochondrostoma olisiponense* Gante, Santos & Alves, 2007 (Veríssimo et al. 2018; Magalhães et al. 2023; Riccioni et al. 2025).

Despite their importance, fish communities in inland wetlands remain poorly characterized, with surveys being biased towards the mainstem (e.g. Rivaes et al. 2025), or outdated and restricted to protected areas, such as Paul do Boquilobo (Collares-Pereira et al. 1994; Correia and Teixeira 2003). Therefore, the role of inland wetlands as refuges for threatened endemics or as reservoirs of invasive species in the region remains largely unknown.

In this study, we combined remote sensing with field surveys to assess fish communities in inland wetlands in the Lower Tagus Basin. Specifically, we aimed to assess (i) the distribution of inland wetlands across the basin; (ii) the use of inland wetlands by native fishes, particularly the endemic *I. olisiponense*, and by non-native fishes, and (iii) examine the relationships between fish communities and environmental contexts. We discuss the implications of our findings for the design of conservation management plans for native fish diversity in highly altered inland wetlands.

Methods

Study area

The study was conducted in the freshwater realm of the Lower Tagus Basin, Portugal, between Golegã and Lisbon (Fig. 1). The alluvial plain is approximately 85 km long and 2 to 10 km wide and exhibits a low gradient (~24 cm *per* km), slow flow, and side channels along the mainstem (Azevêdo et al. 2004; Vis and Kasse 2009; Fernandes et al. 2020). Precipitation is highly seasonal, with 75% occurring between October and April (Azevêdo et al. 2004; Vis and Kasse 2009; Feio and Ferreira 2019).

Wetland selection

Prior to study site selection we conducted an inventory of wetlands across the area ≤ 50 m above sea level (a.s.l.), totaling 3,927.20 km^2 (Fig. 1). Wetlands were assessed as permanent water surfaces using Remote Sensing (RS) and Geographic Information System (GIS) techniques in ArcGIS (Esri® ArcGIS Desktop 10.8.1). To reduce highly reticulated and isolated surfaces, and create a continuous inventory area, a 500 meter *buffer* was added to the elevation limits using a Digital Elevation Model (DEM) with 25 m × 25 m resolution derived from the Shuttle Radar Topography Mission (STRM). Three *Sentinel-2* images, 10 m × 10 m resolution, (https://scihub.copernicus.eu/), covering periods of null rainfall from 8th of August to 10th of October 2019 (https://snirh.apambiente.pt) were used to minimize the inclusion of rain flooded surfaces in the analysis (Perennou et al. 2018). Exact dating was contingent on clear image availability. To delineate water surfaces we used the Normalized Difference Water Index (NDWI), which relies on reflected near-infrared radiation and visible green light to enhance water features while suppressing soil and terrestrial vegetation (McFeeters 1996).

After a thorough interpretation of the images, water surfaces were identified, manually georeferenced using GoogleEarth®, and screened for their potential to regularly sustain fishes using the viewing feature Historical Imagery® on Google Earth images for 2006–2021. Focus was on identifying persistent wetlands which may be used as feeding, reproduction, and also refuge habitats by fishes

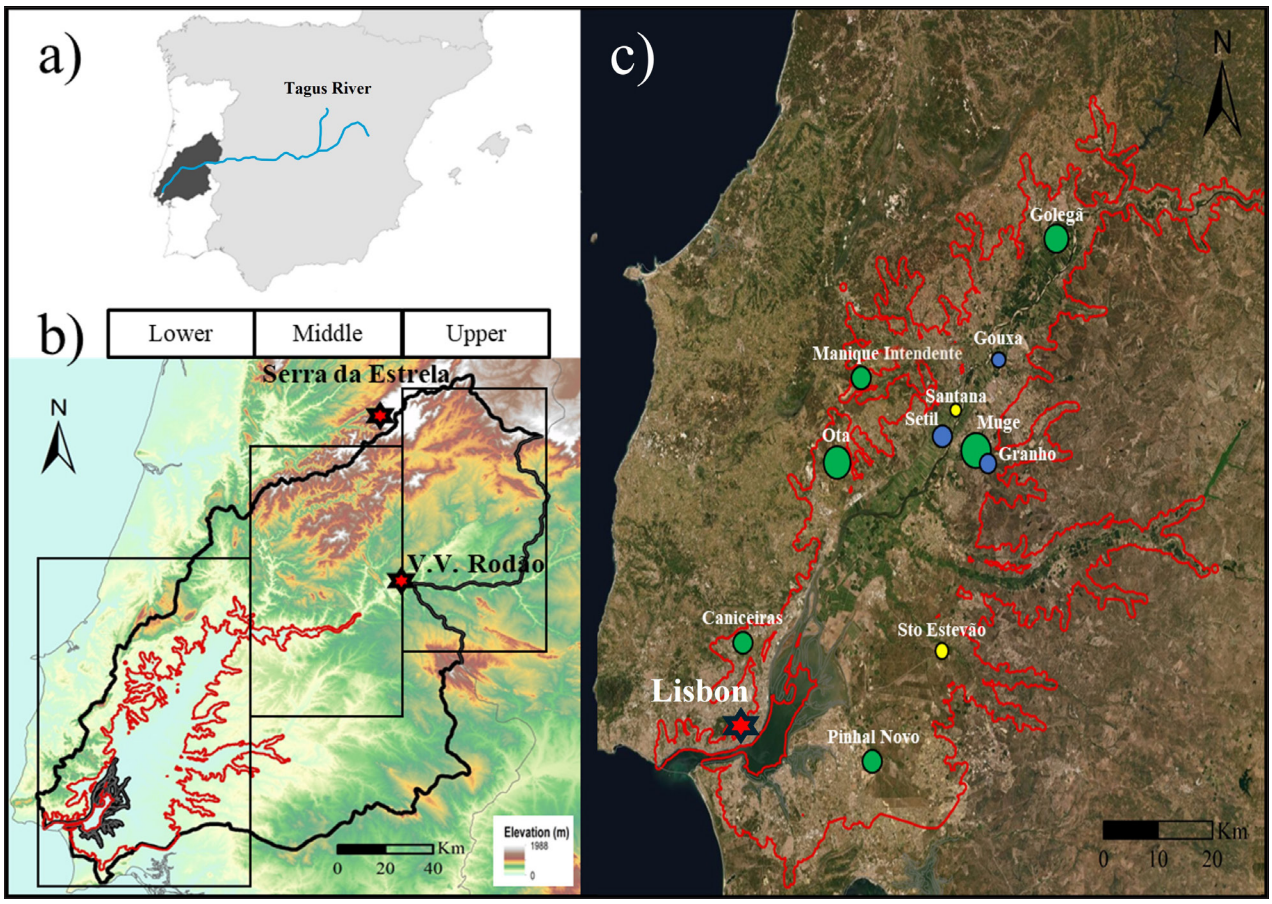

Figure 1. Maps showing the location of **a.** The Tagus River in the Iberian Peninsula and the Tagus River Basin in Portugal (dark grey); **b.** Upper, Middle, and Lower sections of the Portuguese Tagus basin, and (c) the limits of the study area (red) and distribution of the wetlands selected for study, categorized into small 0.5–2.4 ha (yellow), medium 2.5–5.0 ha (blue), and large > 5.0 ha (green). Circle sizes are proportional to wetland area (Source: ArcGIS Base map).

over time. Thus, water surfaces that i) had dry out during the past two available years, ii) were highly artificialized (e.g., dammed), iii) isolated (e.g., with weirs or irrigation peats), iv) and less than < 0.5 ha (i.e, too small as refuge) were not considered for analysis. In addition, we also discarded water surfaces > 50.0 ha to avoid further constraints in sampling.

In total, 30 wetlands were retained and surveyed for accessibility and gear and operator safety (e.g., presence of wild cattle). From these, 11 wetlands were selected for fish and environmental assessment, and categorized into small (0.5–2.4 ha), medium (2.5–5.0 ha) and large (> 5.0 ha) for sampling design (Fig. 1).

Fish sampling

Fishes were sampled between May and June 2021, using a combination of electrofishing, beach seine net, and minnow traps to increase species detectability and catchability in each wetland and maximize fish richness and captures (e.g. Gibson-Reinemer et al. 2017).

Sampling effort was adjusted to wetland area (Table 1). Three transects were electrofished for 10, 20, and 30 minutes in small, medium, and large wetlands, respectively, using electrofishing gear (EL62 II, Hans Grassl, Germany; discharging 300–600V, 2–5 A, DC). Similarly, a beach seine net (15 m long,

Table 1. Fishing techniques used in small (0.5–2.4 ha), medium (2.5–5.0 ha) and large (>5.0 ha) wetlands in the Lower Tagus Basin, with indication of total area (m^2) and total time (min) of sampling. Wetlands are ranked from up to downstream position (Fig. 1). NA = Not applied due to abundant vegetation.

Wetlands	Area	Electrofishing		Seine nets	Minnow traps
		Area (m^2)	Time (min)	Area (m^2)	Total time (min)
Golegã	Large	2,100	90	800	4,590
Gouxa	Medium	800	60	80	2,520
Manique Intendente	Large	1,850	90	1,450	3,780
Santana	Small	600	30	150	1,500
Muge	Large	900	90	450	3,240
Granho	Medium	1,700	60	400	2,520
Setil	Medium	900	60	300	2,400
Ota	Large	1,250	90	600	3,600
Sto Estevão	Small	800	30	450	2,160
Caniceiras	Large	1,300	90	750	3,510
Pinhal Novo	Large	2,300	90	NA	1,080

1.20 m height, and 2.5 mm mesh) were used for dragnetting at one, two, or three locations, and pairs of minnow traps, (60x25 cm, 15.0 mm mesh, and 45x25 cm, 2.0 mm mesh), were set at three, six, and nine locations, in small, medium, and large wetlands, respectively. Minnow traps were baited with commercial Wellmix Boilies® (monster crab flavour) and set at the start of sampling and retrieved afterwards, between 10:00 a.m. and 18:30 p.m., with submerged times ranging from 180 to 510 min. Fishes were identified to species level, counted, and native species were returned to the wetland whereas non-natives were euthanised with an overdose of clove oil (BIO-VERT®), in compliance with national and European regulations on handling wild animals (Portuguese, Decreto-Lei n.º 92/2019; European Union, Directive 2010/63/EU).

Environmental sampling

Prior to fish sampling, we characterised habitat conditions at each wetland using nine variables (Table 2). We measured temperature (ºC), conductivity (mS/cm), dissolved oxygen (% and mg/L), pH, and chlorophyll α (mSPU) using a multiparametric probe (YSI EXO2 Multiparameter Water Quality Probe), and turbidity using a Secchi Disk (cm). Depth (cm) was measured using a portable water depth sounder gauge (Vexilar LPS-1). Vegetation cover (i.e., aquatic vegetation, branches, or roots) was visually assessed. Depending on wetland area, measurements were taken at five, six, or nine points covering perceived variability in local conditions.

We further used five variables to characterize landscape context for each wetland (Table 2). Wetlands were evaluated for connectivity to the nearest watercourse *in situ* and categorized as: 1 – Paleopotamic (i.e. isolated from the watercourse), 2 – Plesiopotamic (i.e. susceptible to watercourse flooding), and 3 – Parapotamic (i.e. directly connected to the watercourse) (Ward and Stanford 1995). Wetland area (ha), elevation (m), and Strahler stream order of the nearest watercourse (km) were derived from a Digital Elevation Model (DEM). Hydrological distance to the Tagus River was determined along the drainage network using the Google Earth measurement tool.

Table 2. Environmental conditions in inland wetlands in the Lower Tagus Basin, between May and June of 2021. For each variable, the units, type of transformation, and code are indicated. Variables retained for analysis are in bold, and * denotes variables discarded from canonical ordination.

Variables (units, transformation)	Code	Mean ± Std dev	Range (min – max)
Temperature (ºC, log10)	TEMP	20.7 ± 1.4	16.3–22.9
Conductivity (mS/cm, log10)	COND	0.570 ± 0.229	0.255–1.095
Dissolved oxygen (%, arcsin√p)	O2%	84.3 ± 37.5	3.9–158.4
Dissolved oxygen (mg/L, log10)	$O2_{(mg/L)}$	7.5 ± 3.3	0.4–14.5
pH (log10)	PH	7.7 ± 0.6	6.5–9.5
Chlorophyll α (mSPU, log10)	CHA	28.7 ± 20.8	3.2–75.0
Secchi (cm, log10)	SCH	46.4 ± 48.2	5.0–180.0
Depth (cm, log10)	DEP	98.9 ± 93.2	20.0–528.0
Vegetation Cover (%, arcsin√p)	CVR	78.5 ± 11.2	66.7–100.0
Connectivity (log10)	CONN	2.1 ± 0.8	1–3
Area (ha, log10)*	AREA	4.7 ± 2.5	0.5–9.0
Elevation (m, log10)*	ELEV	10.4 ± 10.3	2.0–35.0
Stream order (log10)	SORD	2.5 ± 1.4	1–5
River distance (Km, log10)	RD	17.0 ± 11.9	2.5–46.8

Data analysis

Data analysis focused on describing environmental gradients among wetlands, assessing local fish species richness and abundance, and relating variation in community structure to environmental variables.

A Principal Component Analysis (PCA) was used to summarize the main environmental gradients among wetlands (McCune et al. 2002). Prior to analysis, variables were scanned for outliers and strong asymmetry and transformed using Log10 or arcsine of the square root for percentages (Table 2). To avoid multicollinearity issues, pair-wise Pearson correlation between variables was determined, and for highly correlated (r >|0.60|) pairs, only the variable most relevant to the interpretation of fish patterns, as derived from the literature, was retained for analysis (Zuur et al. 2010).

Fish abundance at each wetland was quantified using the MultiGear Mean Standardization (MGMS) method (Gibson-Reinemer et al. 2017). This method preserves the species structure within and among sites by keeping values of catchability for each gear constant and maintains species abundance by weighting rare and abundant species equally during data transformation, thereby providing a robust basis for multivariate analyses (Gibson-Reinemer et al. 2017). Fish data were first standardized as catch *per* unit of effort (CPUE), using both gear catchability and sampling effort. Based on the total number of individuals captured, catchability coefficients were assigned as 1 for electrofishing (5,270 fishes), 0.5 for seine nets (2,428 fishes), and 0.1 for minnow traps (574 fishes). Sampling effort was defined as total electrofishing time (minutes), total area (m^2) sampled by seine nets, and submerged time (minutes) per pair of minnow traps (Table 1). CPUE values were then combined into a MGMS matrix of species by wetland. Hereafter, the standardized fish data are referred to as MGMS catches.

Variation in fish community structure was related to environmental variables using Canonical Correspondence Analysis (CCA). A uni-modal model of ordination was used because preliminary Detrended Correspondence Analysis (DCA)

exhibited turnovers < 2 SD, indicating a relatively long ecological gradient and suggesting predominantly unimodal species responses (ter Braak and Verdonschot 1995; Lepš and Šmilauer 2006). To dampen the influence of zeroes in the species matrix, MGMS catches were Hellinger transformed (Borcard et al. 2011). Only environmental variables with variation inflation factors less than 5.0 were used in model building to improve interpretability of canonical axes and reduce unstable estimates (O'Brien 2007). The statistical significance of the overall model, the first ordination axes, and individual environmental variables were determined by Monte Carlo permutations tests (999 unrestricted permutations). Analyses were carried out in R software (version 4.2.2), using the *vegan* package (Oksanen et al. 2012), and the significance of statistical testing was assessed at $p < 0.05$.

Results

Wetland distribution

In total, 409 water surfaces were identified, of which 94 were inadequate in size (< 0.5 ha or > 50.0 ha), 54 were heavily artificialized, and 32 had dried out during the last two years. Among 30 water surfaces with potential to sustain fishes, 19 lacked access and safe conditions for sampling. The 11 wetlands selected for assessment were distributed across the landscape, six on the right and five on the left margin of the Tagus River, ranging in area between 0.5 and 9.0 ha, and covered a total of 51.2 ha (Fig. 1).

Environmental gradients

The PCA extracted two axes with eigenvalues higher than 1, accounting for 61% of the total variation in the data (Fig. 2). PC1 (40% of total variation) primarily represented a gradient of connectivity (loading: 0.760) in opposition to elevation (-0.798) and area (-0.674), whereas PC2 (21% of total variation) reflected the coordinate variation in conductivity (0.726) and vegetation cover (0.699) among wetlands.

Fish richness and abundance

Fishes were captured in all wetlands except Pinhal Novo (henceforth not considered for the fish results), totaling 8,272 individuals from five native and eight non-native species (Table 3). The number of species per wetland ranged from three to eight species (Mean ± SD: 5.3 ± 1.8). Native fishes were absent in Santana and Muge, and in the remaining wetlands ranged between one and three species (1.2 ± 0.9). Non-native species were found in all wetlands, ranging in number between two and seven species (4.1 ± 1.7). Total catches per wetland ranged from 16 to 3,567 fishes (Table 3).

Gambusia holbrooki Girard, 1859 was the most caught species (4,769 individuals), occurring in all wetlands, followed by *Lepomis gibbosus* Linnaeus, 1758 (652 individuals) occurring in half the wetlands (Fig. 3). *Ameiurus melas* Rafinesque, 1820, *Carassius* sp. Jarocki, 1822, and *Anguilla anguilla* Linnaeus, 1758 were also often captured (≥ 50% of wetlands) but in small numbers (163, 140, and 35 individuals, respectively). The frequency of occurrence was lower for *Cyprinus carpio* Linnaeus, 1758 (40%), *Micropterus nigricans*

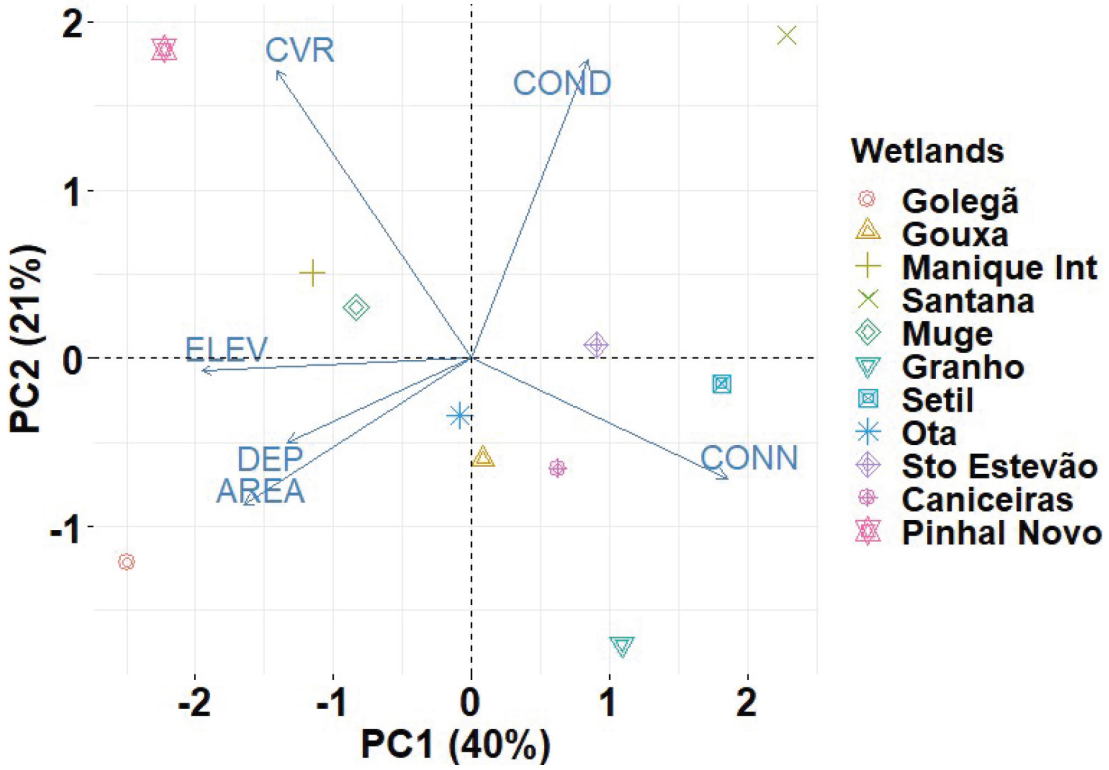

Figure 2. Principal Components Analysis (PCA) of environmental variables for wetlands in the Lower Tagus Basin, between May and June of 2021. Variable codes present in Table 2.

Table 3. Fish species richness and abundance (MGMS catches) for natives (with endemic species = END) and non-natives (with invasive species = INV) in wetlands of the Lower Tagus Basin between May and June of 2021, with indication of mean ± standard deviation and the range (minimum–maximum). NC = No fish captured.

Wetlands	Richness			Abundance	
	Overall	Natives	Non-natives	Natives (END)	Non-natives (INV)
Golegã	7	2	5	15 (0)	1,507 (640)
Gouxa	6	1	5	9 (0)	469 (416)
Manique Int.	3	1	2	1 (0)	56 (56)
Santana	3	0	3	0 (0)	284 (284)
Muge	4	0	4	0 (0)	3,567 (3567)
Granho	8	1	7	4 (4)	246 (243)
Setil	6	2	4	136 (0)	196 (192)
Ota	4	1	3	3 (0)	1,512 (323)
Sto Estevão	7	1	6	47 (0)	187 (186)
Caniceiras	5	3	2	17 (8)	16 (16)
Pinhal Novo	NC	NC	NC	NC	NC
Mean ± Std Dev	5.3 ± 1.8	1.2 ± 0.9	4.1 ± 1.7	23.2 ± 42.1	804.0 ± 1,118.3
Range (min–max)	(3–8)	(0–3)	(2–7)	(0–136)	(16–3,567)

Cuvier, 1828 (40%), and *Alburnus alburnus* Linnaeus, 1758 (30%), but their catches were high (1,189, 866, 161 individuals) in only one wetland (Fig. 3). *Luciobarbus bocagei* Steindachner, 1864 and *Cobitis paludica* de Buen, 1930 were both sparse (<20% of wetlands) and rare (< 3 individuals). The endemic *I. olisiponense* was only found in two wetlands (Granho and Caniceiras) in low numbers (4 and 8 individuals; Fig. 3).

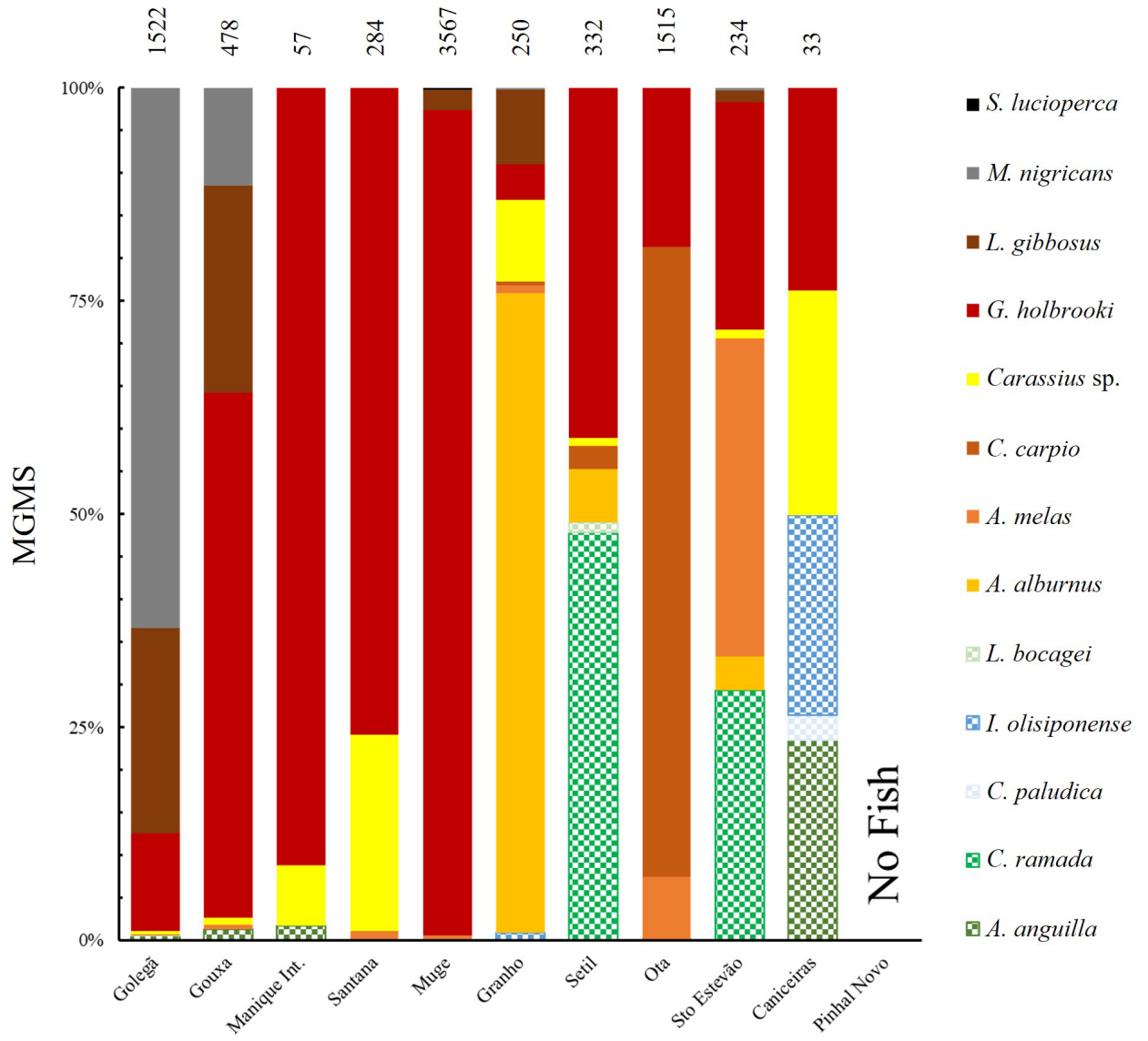

Figure 3. Variation in fish communities among wetlands of the Lower Tagus Basin between May and June of 2021, as derived using the Multi Gear Mean Standardization (MGMS). The number of fishes captured is indicated above the bars, native species are represented by pattern and non-native by full bars.

Fish community structure

The CCA revealed significant effects of wetland connectivity, conductivity, depth, and vegetation cover on fish community structure (Fig. 4). The overall model (p = 0.002) and all environmental variables were statistically significant ($p \leq 0.005$). The ordination space defined by the first two canonical axes ($p \leq 0.01$) accounted for about 69% of the total variation in species-environment relations, and represented 65% of the variation in species data. The first axis mainly reflected the tendency for native *Chelon ramada* Risso, 1827, and non-native *A. melas*, *A. alburnus*, and *C. carpio* to increase in connected wetlands with high-conductivity waters in contrast to non-native *M. nigricans* and *L. gibbosus*. The second axis was mainly related with depth and reflected the association of non-native *C. carpio* and *M. nigricans* with deeper wetlands and native *I. olisiponense* and *L. bocagei* and non-native *A. alburnus* with shallower wetlands (Fig. 4).

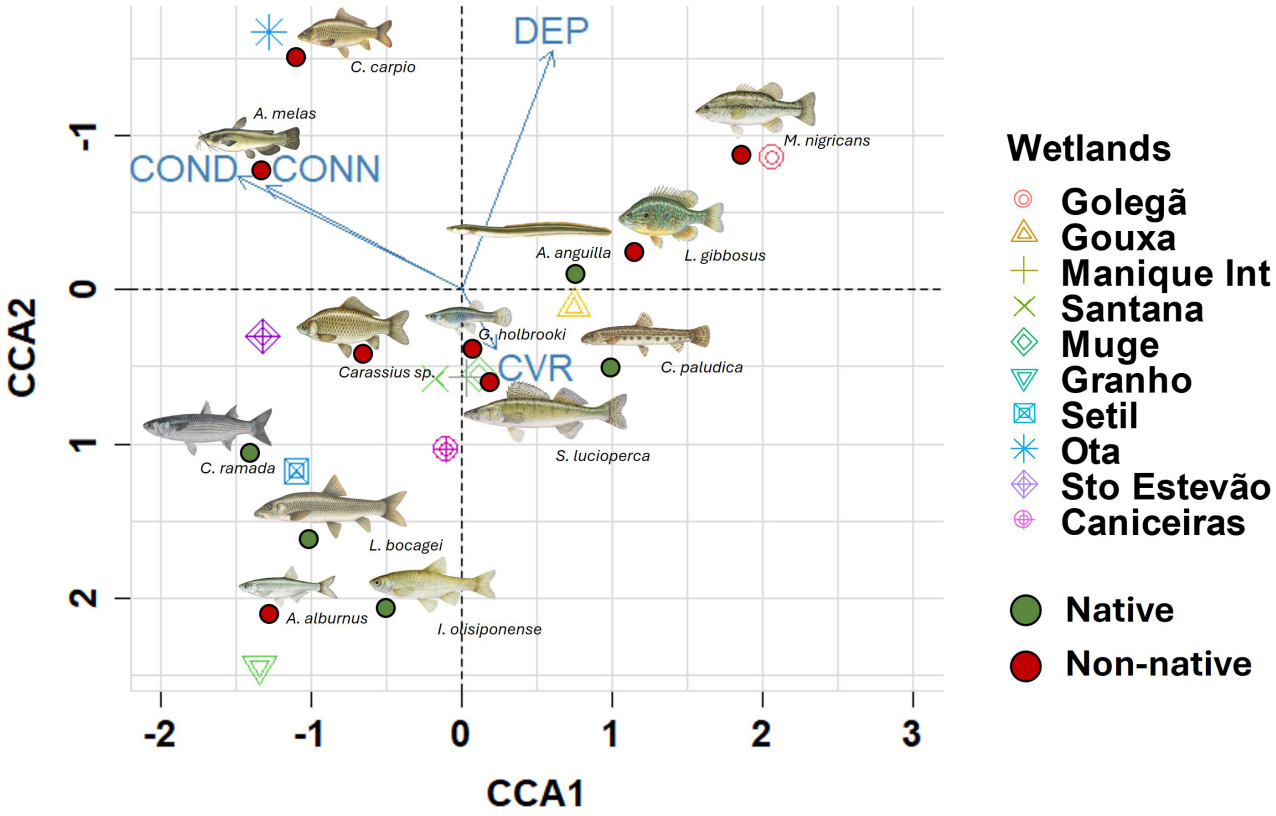

Figure 4. Canonical Correspondence Analysis (CCA) ordination diagram depicting the effects of environmental variables on fish communities in inland wetlands (excluding Pinhal Novo) in the Lower Tagus Basin between May and June of 2021. Variable codes are in Table 2. Fish scientific illustrations copyrights to Cláudia Baeta®.

Discussion

Using remote sensing and field surveys, we updated the distribution of inland wetlands in the strongly altered Lower Tagus Basin and assessed local fish communities. We found that inland wetlands i) were spread across the landscape; ii) were used mainly by non-native fishes, though still harbored some native species including *I. olisiponense*, and iii) connectivity, conductivity, and depth shaped local fish community structure. Overall, although the differences are not significant, native migratory species and threatened regional endemics appear to mainly occur in parapotamic and shallow wetlands, which should thus be prioritized for conservation management.

Inland wetlands in the Lower Tagus Basin

Based on the Normalized Difference Water Index (NDWI) we identified 409 water surfaces in the Lower Tagus Basin, of which 30 were classified as inland wetlands with potential to sustain fishes. This surpasses the total advanced by Farinha and Trindade (1994) of eleven wetlands, indicating that wetlands may be more prevalent in the region than previously thought.

Remote sensing is independent of land accessibility and property, and thus likely to allow more complete inventories of inland wetlands than traditional methods (Perennou et al. 2018). Nevertheless, some additional improvements in approach may still enhance the assessment of inland wetlands in the Lower

Tagus Basin. The use of automated or semi-automated methods can reduce or even eliminate constraints associated with the use of Google Earth Historical images which are unevenly distributed across the region and over the years (Lefebvre et al. 2015). Moreover, accounting for dense aquatic vegetation, and particularly for invasive water hyacinth (*Eichhornia crassipes*) may avoid underestimation of water surfaces using NDWI (Gao 1996; Perennou et al. 2018).

Fish communities in the Lower Tagus wetlands

Our surveys confirmed that inland wetlands in the Lower Tagus Basin are used by multiple fish species, as previously suggested by Correia and Teixeira (2003). However, local communities were largely dominated by non-native species, with native and endangered species being much less common and abundant than in the past (e.g. Collares-Pereira et al. 1994; Correia and Teixeira 2003). This pattern is unlikely to be associated with sampling insufficiencies given multi gears have been used to sample fish communities and cover variability in habitat conditions (Gibson-Reinemer et al. 2017) and this pattern is consistent with that found across the Tagus Basin (Martelo et al. 2021; Rivaes et al. 2025). Nevertheless, further surveys using additional techniques are encouraged to confirm the decline of fish diversity in the region.

Wetlands appeared to function as reservoirs for non-native fishes, which promotes already considerable biotic homogenization of local communities. In particular, invasive *A. melas*, *G. holbrooki*, and *L. gibbosus*, recognized as tolerant to a broad range of environmental conditions (Cucherousset et al. 2007; Ribeiro et al. 2008), are already widespread and abundant, similar to what has been found in inland wetlands in France and Spain (Cucherousset et al. 2008; Clavero et al. 2021). Other non-native species such as *M. nigricans* are still mostly associated with paleopotamic wetlands (Golegã and Gouxa), reflecting at least some local introductions by anglers (personal observation), but have the potential to further spread given the high value of these non-native species for angling (Collares-Pereira et al. 2021; Banha et al. 2024).

The dominance of non-native fishes in wetlands may be detrimental not only for native fishes, which tend to be outcompeted by *G. holbrooki*, *L. gibbosus*, and *Carassius gibelio* Bloch, 1782 (Rincón et al. 2002; Gkenas et al. 2022; Tapkir et al. 2022), but also for other vertebrates, such as amphibians and waterbirds, which may be preyed upon by *M. nigricans* and *Sander lucioperca* Linnaeus, 1758 (Godinho et al. 1997; Ribeiro et al. 2021). Besides, by destroying macrophyte beds, *C. carpio* may also have negative impacts on threatened waterbirds, as found in SW Spain (Maceda-Veiga et al. 2017).

Although in reduced numbers, some native and threatened fishes still used inland wetlands in the Lower Tagus Basin. These included *C. paludica*, listed as Least Concern (LC), *C. ramada* and *L. bocagei*, listed as Near Threatened (NT), *I. olisiponense*, listed as Endangered (EN), and *A. anguilla*, listed as Critically Endangered (CR) (IUCN 2026). Parapotamic wetlands with high-conductivity waters (Setil and Sto Estevão) were favoured by *C. ramada*, likely reflecting its feeding migration that can proceed several kilometres upstream in the Tagus Basin (Pereira et al. 2021). Conversely, *I. olisiponense* was associated with shallow wetlands (Caniceiras and Granho), likely using them for spawning, feeding, and nurseries (Veríssimo et al. 2018). This is consistent with previous studies

indicating that this species prefers lentic and shallow waters, including seasonally flooded areas (Veríssimo et al. 2018; Riccioni et al. 2025), and similar to what has been found for other wetland species whose current distribution shrinks from dynamic floodplains to remnant oxbows and pools (Ribeiro et al. 2004; Moyle et al. 2007; Šmejkal et al. 2025; Lelièvre et al. 2026). Patterns for other species were less clear and deserve further analysis.

Future studies should not only extend to unsampled inland wetlands with potential to sustain fishes already identified in the Lower Tagus but also cover multiple seasons. Indeed, different species have been found to use inland wetlands in Central California over the year (Moyle et al. 2007), and this may also be the case here, given the recent records of *Gasterosteus aculeatus* Linnaeus, 1758 in the Caniceiras in the summer of 2021 (personal observation). It will also be important to clarify whether fishes are indeed absent in Pinhal Novo, given that the lack of captures in the present study may be circumstantial or even be due to sampling constraints. The relative importance of inland wetlands as feeding, nurseries, and refuge areas for endangered endemic *I. olisiponense* deserves particular attention given its association to these habitats, reflecting a long and historical use as recently suggested by Riccioni et al. (2025). Use of additional techniques, such as gill nets in wetlands > 1 m deep (Sánchez-González and Casals 2022) and environmental DNA metabarcoding may enhance fish community assessments (Antognazza et al. 2021; Kačergytė et al. 2021; Curto et al. 2025), and in combination with citizen science data may help engage local public and stakeholders in biodiversity conservation (Newman et al. 2017; Martelo et al. 2021; Dias et al. 2025).

Implications for conservation

Inland wetlands in the Lower Tagus have deserved increased attention in recent years. The classification of Gouxa and Paul das Caniceiras as Local Natural Reserves recognize, respectively, the occurrence of priority habitats integrated in the EU Habitats Directive and the importance of water bird communities and the occurrence of *I. olisiponense*. Despite the high landscape perturbation and the prevalence of non-native species in local fish communities, the occurrence of *A. anguilla* in many wetlands, of *I. olisiponense* in Caniceiras and Granho, and of *G. aculeatus* also in the former, reinforce the importance of inland wetlands as refuges for native and threatened fishes. In these circumstances, it will be important to recognize these wetlands as a priority in conservation planning.

Conservation of wetlands in the Lower Tagus Basin should include restoration actions focusing on habitat enhancement, pollution control, water abstraction regulation, and control of exotic and invasive aquatic vegetation to rehabilitate wetlands for native fishes (e.g. Benejam et al. 2010; Carvalho et al. 2019; Radinger et al. 2023). The recent EU Nature Restoration Law offers an important path to recover wetlands in this region by increasing the water-level on a more permanent basis, which will be essential to create and safe-guard areas for endangered fishes. Wetlands might also benefit from control actions directed at invasive fishes, which have led to native fish recovery elsewhere (Britton and Brazier 2006; Bosch et al. 2019; Martínez et al. 2022). Involvement of stakeholders, such as landowners, farmers, and local municipalities, and environmental outreach may also be key to promoting sustainable wetland management.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Fishes were handled according to ethical approval under the fishing license reference number 504/2021/CAPT, emitted on March 16th, 2021, obtained by the Portuguese Institute for Nature Conservation and Forests (Departamento de Conservação da Natureza e Biodiversidade). Species were identified, counted, and native species returned to the wetland whereas non-natives were euthanised with an overdose of clove oil (BIOVERT®), in compliance with National and European regulations on handling wild animals (Portuguese, Decreto-Lei n.º 92/2019; European Union, Directive 2010/63/EU).

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Conceptualization: DR, FR, JC, MFM. Data curation: DR. Methodology: DR, FR, JC, MFM. Investigation: DR, DD, JG, JM, LMC, CDS, FR, MFM. Writing—original draft preparation: DR, FR, MFM. writing—review and editing: DR, DD, JG, JM, RR, LMC, CDS, FR, JC, MFM. Formal analysis: DR, RR. Visualization: DR, RR. Supervision: FR, MFM. Funding acquisition: FR. All authors have read and agreed to the published version of the manuscript.

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Data availability

Data on surveyed inland wetland fish communities are openly available on GBIF to support FAIR data principles. Ribeiro D (2026). Assessing the use of Inland Wetlands by fish in the Lower Tagus Basin (Portugal). MARE - Marine and Environmental Sciences Centre. Sampling event dataset https://doi.org/10.15468/xjzvgu. All other data that support the findings of this study are available in the main text.