

Seasonal differences in drivers of species richness of waders in inland wetlands of La Mancha Húmeda Biosphere Reserve

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Abstract

1. Temporary inland wetlands are among the most threatened ecosystems worldwide, and recognition of the factors that determine species richness in different seasons is key for developing conservation plans for these systems. La Mancha Húmeda Biosphere Reserve in central Spain has many inland wetlands of this type, but the driving ecological processes of species richness are poorly understood.
2. This study examines the association of landscape and local variables with species richness patterns of inland wetlands of La Mancha Húmeda Biosphere Reserve during winter and the breeding season. The number of lakes in several increasing radii was a proxy of connectivity, and maximum flooded surface and shoreline length were surrogates of the species–area relationship.
3. Other landscape and local habitat variables, such as hydroperiod (length of inundation period), distance from human settlements, shoreline development index, vegetation surface cover, average lake depth, number of islands and surface area of islands were also analysed. Hierarchical partitioning analysis was used to evaluate the contribution of the environmental variables to explain the species richness of waders.
4. Species richness (26 species, four threatened in Europe) had different associations with the variables during the wintering and breeding seasons. The richness of breeding and wintering species was positively associated with hydroperiod and maximum flooded surface area respectively. No variable measured was negatively associated with species richness in any season.
5. Hydroperiod and flooded surface area are altered directly by human activities. Water extraction for irrigation reduces hydroperiod in some wetlands, whereas wastewater input extends hydroperiod in others, promoting wader concentrations in lakes flooded in summer and potentially favouring botulism outbreaks. In addition, the lack of protection and management on most of the lakes in La Mancha Húmeda Biosphere Reserve also favours encroachment of agriculture, destroying and degrading habitat for wintering and breeding waders.

KEYWORDS

conservation, continental wetlands, flooded surface, human activities, hydroperiod, Iberian Peninsula, seasonal variation, temporary lakes, wader species richness

1 | INTRODUCTION

Natural inland wetlands are among the most threatened ecosystems worldwide (Kingsford, Basset, & Jackson, 2016). Understanding drivers of ecological patterns and processes is critical to effective biodiversity conservation. In particular, inland wetlands form habitat patches or fragments across landscapes, allowing analysis of the mechanisms to be investigated. Two processes drive richness patterns in isolated habitat patches: increases with the size of the area and decreases with isolation (Cook, Lane, Foster, & Holt, 2002; Prugh, Hodges, Sinclair, & Brashares, 2008). Many other integrated processes can also drive species richness patterns (Keil et al., 2012; Skórka, Martyka, & Wójcik, 2006). Degradation or habitat fragmentation may alter the shape and connectivity of patches by reducing the total area available at the landscape scale (Fahrig, 2003) and decreasing species richness (Guadagnin & Maltchik, 2007; Guadagnin, Maltchik, & Fonseca, 2009; Peintinger, Bergamini, & Schmid, 2003). This problem may be accentuated for continental natural wetlands, where habitat loss is more rapid than in coastal wetlands (Davidson, 2014).

La Mancha Húmeda Biosphere Reserve (hereafter referred to as MHBR) in the central Iberian Peninsula is characterized by inland wetlands of high conservation value in Europe. The reserve was established in 1980 and includes more than 25,000 ha of temporary and permanent wetlands (Crespo, García, & Bravo, 2011). Many inland wetland types occur in the reserve, varying significantly in shape, area, hydroperiod (length of inundation period), habitat characteristics, biodiversity and threats (Doña et al., 2016; Florín & Montes, 1999; Hera & Villarroya, 2013). Most of these wetlands are classified as Ramsar Sites and Important Bird Areas (Crespo et al., 2011; Infante, Fuente, & Atienza, 2011). In addition, most of the wetlands of the MHBR are also designated within two Natura 2000 sites. These share the same name – Humedales de la Mancha – one is a Special Protection Area (SPA; code ES0000091) designated under the Birds Directive (Council of the European Communities, 2010) and the other is a Special Area of Conservation (SAC; code ES4250010) designated under the Habitats Directive (Council of the European Communities, 1992; Cubero-Rivera, 2015). At a national level, Spain has protected some of these wetlands as Natural Parks and Natural Reserves. However, despite their environmental importance, the landscape has been drastically transformed by agriculture (mainly vineyards, cereal crops and olive groves), and by forestry and pasture land (Crespo et al., 2011). Furthermore, the water regime of these wetlands has changed considerably owing to the overexploitation of aquifers for irrigated agriculture and wastewater inputs from adjacent urban areas (Gonçalves et al., 2016; Martínez-Santos, De Stefano, Llamas, & Martínez-Alfaro, 2008).

Waterbirds use multiple habitats seasonally, playing a vital role in the exchange of nutrients between ecosystems, and structuring ecological communities (Green & Elmgberg, 2013). Seasonal variations in waterbird richness may reflect different processes, such as changes in environmental conditions, seasonality of migratory movements and local displacement of resident species (Dalby, McGill, Fox, & Svenning, 2014; Guadagnin, Peter, Perello, & Maltchik, 2005; Sebastián-González, Sánchez-Zapata, & Botella, 2010; Tomankova, Boland, Reid, & Fox, 2013). In the MHBR region, the variability of rainfall during the

breeding season affects the temporal abundance of resident species, which may be forced to move to other wetlands in the late summer, returning in the winter (Gonçalves et al., 2016). On the other hand, whereas most of the migratory populations use the region as a stop-over site, species such as dunlin (*Calidris alpina*) and little stint (*Calidris minuta*) occupy the region all winter (Birdlife International, 2015). In addition to species' phenology, other factors commonly linked to species richness can also vary between seasons. For example, during the wintering period, species prioritize sites for foraging and resting, but are more selective during breeding, requiring safe environments for nesting and suitable habitats for foraging (Cherkaoui, Hanane, Magri, Agbani, & Dakki, 2015; Hamza, Hammouda, & Selmi, 2015; Pino, Roda, Ribas, & Pons, 2000; Sebastián-González et al., 2010).

Effective conservation of wetlands depends on understanding how these factors affect species richness between different seasons (Ma, Cai, Li, & Chen, 2010). The aims of this study were to identify the effects of landscape and local factors on wader species richness during wintering and breeding seasons in inland wetlands of the MHBR. In addition, this article considers the conservation status of these wetlands, highlighting the degree of protection and the inefficiency of the management plans in maintaining this important ecosystem in the central Iberian Peninsula.

2 | METHODS

2.1 | Study area

The MHBR is in Castilla-La Mancha, central Spain (Figure 1), an extensive semi-steppe landscape on slightly undulating and predominantly agricultural terrain (Crespo et al., 2011). In general, MHBR wetlands are shallow, saline and in closed drainage basins (endorheic), where water flows to a central point and is temporarily retained (Castillo-Escrivà, Valls, Rochera, Camacho, & Mesquita-Joanes, 2017; Crespo et al., 2011). The region experiences an average temperature of 14.7°C and average annual rainfall of 300–500 mm (Martínez-Santos et al., 2008), with low to no precipitation levels in summer (July–October). Thus, the wetlands are usually hydrologically stable between January and February after autumn and early winter rains, with some water usually remaining until mid-summer (Gonçalves et al., 2016). This is strongly altered in some sites by wastewater input, which prolongs the hydroperiod and changes physical–chemical conditions from hypersaline to fresh water (Castillo-Escrivà et al., 2017).

2.2 | Bird survey protocol and migration status

Twenty-three lakes formally included in national and/or international protection zones were selected for the study (Tables 1 and 2). The lakes were monitored monthly (October 2010–February 2014), with 10 lakes also monitored over a longer period, starting in October 2006. Counts were made in the last week of each month (08:00 h–12:00 h), when climatic conditions were favourable (with little wind or no rain). In each lake, the same researcher counted birds (using telescopes of 20–60 × 65 and 20–60 × 80) from fixed observation points that provided the best views of the lake area.

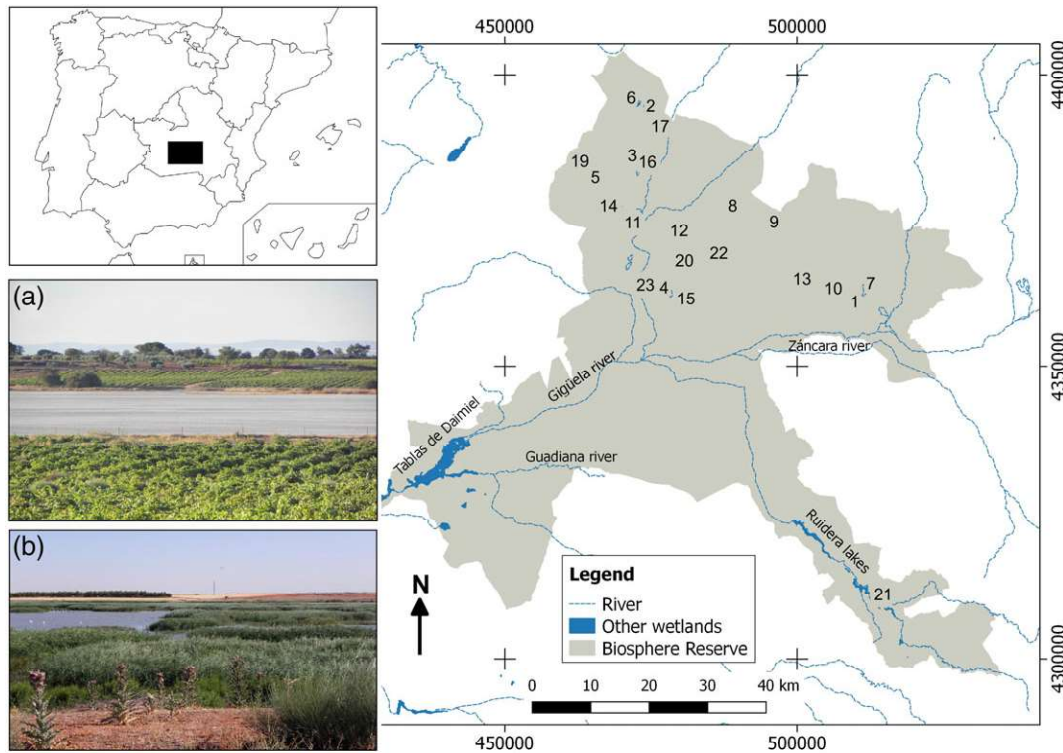


FIGURE 1 Location of the 23 lakes (identification codes are in Table 1) monitored in La Mancha Húmeda Biosphere Reserve, central Spain. (a) Alcahozo lake (lake 1), a saline lake marked by a short annual hydroperiod, without influence of wastewater and surrounded by extensive vineyards. (b) Pedro Muñoz lake (lake 10), a typical lake with wastewater input, marked by a long annual hydroperiod and dense aquatic vegetation at the edge

Following BirdLife International (2017), species were classified into three categories, reflecting their temporal pattern of habitat use in the Iberian Peninsula: resident (using a habitat throughout the year, including for breeding), breeding (species present only in the breeding season), and nonbreeding (using a habitat, but not normally for breeding). For the breeding season, only breeding and resident waders with occurrences in May, June and July were included (comprising 21 monthly counts for the lakes monitored in the extended period and nine counts for the rest of the lakes). For the wintering period, all species with occurrences in December, January and February were analysed (comprising 24 counts for the lakes monitored in the extended period and 12 samples for the rest).

2.3 | Environmental variables

Thirteen environmental variables were analysed per lake (Table 1). They were separated into two groups: (i) landscape variables (distance from human settlements and number of lakes within three radii: 2, 5 and 10 km), and (ii) local variables (hydroperiod – length of inundation period calculated as the percentage of months with water [October 2010–February 2014] – shoreline length, shoreline development index, average lake depth, total lake surface area, maximum flooded surface area, surface area with natural vegetation surrounding the lake, number of sedimentary islands and total surface area of sedimentary islands). Maximum flooded surface area was defined by the vegetation marking the edge of lakes. Similarly, shoreline length is the perimeter along a lake's edge added to the perimeter of the

sedimentary islands. The shoreline development index D_L is the ratio between the total shoreline length (lake's edge plus island edges) and its shoreline length if it were circular with the same area (Kent & Wong, 1982; $D_L = L/2(\pi A)^{1/2}$, where L is the lake shoreline length and A the lake area). The average depth is the difference between the average of the altitude above sea level at the four cardinal points on the lake's edge and the altitude of the deepest point of the lake. Data for these variables were obtained by fieldwork and from the geographical viewer Iberpix (Spanish National Geographic Institute) and Google Earth Pro Version 2015.

2.4 | Data analysis

As census effort differed among wetlands, sampled-based extrapolation curves (Colwell et al., 2012) calculated with program EstimateS 9.1.0 (Colwell, 2013) were used to estimate total comparable richness in the wetlands, sampled over the short time period. Curves were extrapolated to 21 and 24 samples (months), for the breeding and wintering periods respectively. This procedure made the most of the available information for each wetland, but to check whether the extrapolation was biased the data were also analysed using the same surveys performed in the common census period for all the sites. The results of the latter analyses are presented as Supporting Information. To reduce the effects of collinearity among environmental variables, Pearson's correlation r were calculated; pairs of variables with $r > 0.7$ were identified, and only the variable of most biological importance was retained in the analysis (Table S1). Thus, the total lake

TABLE 1 Twenty-three lakes monitored (2006–2014*, 2010–2014) in La Mancha Húmeda Biosphere Reserve (see Figure 1)

Code	Lake	UTM		Landscape variables				Local variables								
		X	Y	R2	R5	R10	DH	Area	Flood	Veg	Ni	IsA	AD	Hyd	Leng	SDI
1	Alcahozo*	510620	4360164	1	2	6	5,509	88.6	69	19.5	0	0	1.75	58.5	4,805	1.63
2	Altillo Grande	474187	4393670	2	3	4	2,649	32.9	20.4	12.4	0	0	4.25	43.9	2,932	1.82
3	Artevi	472611	4385210	1	1	9	965	27.9	16.7	11.2	0	0	4.75	68.2	3,102	2.14
4	Camino de Villafranca*	478055	4362616	0	2	10	2,263	159.9	134.7	23.7	2	1.7	2.25	95.1	9,181	2.23
5	Campo de Mula	464695	4381452	0	1	6	5,483	50.9	25.5	25.3	0	0	3.25	21.9	4,038	2.25
6	Longar	472448	4395066	2	3	5	1,757	259.5	99.1	160.3	0	0	4	92.6	5,895	1.67
7	Manjavacas*	511840	4363360	1	7	17	6,639	262.8	197.8	64.0	3	9	2.75	97.5	9,872	1.98
8	Mermejuela*	488191	4376617	0	2	5	4,834	9.9	8.6	1.2	0	0	6.5	82.9	1,374	1.31
9	Miguel Esteban	495294	4373855	0	1	1	1,376	92.2	23.4	68.8	0	0	2.5	97.5	3,966	2.31
10	Pedro Muñoz*	504589	4362479	2	3	11	362	41.3	26.1	15.2	0	0	3.25	87.8	5,936	3.27
11	Peña Hueca	470426	4373729	0	2	8	8,880	158.8	132.6	19.6	4	6.6	3.75	58.5	11,146	2.73
12	Quero*	478215	4372367	1	6	16	787	95.7	84.0	11.6	0	0	2	70.7	4,991	1.53
13	Retamar	502427	4364111	0	3	7	2,503	79.1	62.7	16.4	1	4	3.5	21.9	5,217	2.21
14	Tírez	469331	4376605	0	2	6	8,546	131.8	81.1	50.6	1	0.04	4.25	51.2	6,112	1.91
15	Veguilla*	479389	4360715	0	2	7	886	89.0	44.3	44.7	0	0	4.25	97.5	9,607	4.06
16	Larga de Villacañas	472815	4384080	2	3	12	1,458	167.3	114.5	52.7	0	0	3.25	100	9,648	2.54
17	Albardiosa	474994	4390229	0	3	5	5,085	71.8	39.5	32.3	0	0	2.5	8.3	3,557	1.59
18	Altillo Chica	473975	4394727	2	3	5	1,436	24.6	17.8	6.8	0	0	3	55.5	2,200	1.47
19	Camino de Turleque	464403	4384224	0	1	4	4,082	48.6	39.4	9.2	0	0	5.25	5.5	3,097	1.39
20	Pajares*	482321	4367206	0	1	5	4,669	23.5	20.9	2.6	0	0	2.75	39	2,360	1.45
21	Redondilla	513136	4310021	5	9	10	171	5.7	3.5	2.2	0	0	11	26.8	981	1.47
22	Salicor*	485033	4368502	1	2	5	7,161	81.4	48.3	23.7	3	9.2	5.75	55.5	5,159	2.09
23	Yeguas*	475657	4363078	1	3	6	4,683	96.2	64.9	31.3	0	0	2	61.1	4,593	1.6

Six landscape variables: UTM, datum ETRS89; R, number of lakes present in radii of 2 (R2), 5 (R5) and 10 km (R10); DH, distance (metres) from human settlement.

Nine local habitat variables: Area (ha); Flood, flooded surface area (ha); Veg, area covered by natural vegetation (ha); Ni, number of sedimentary islands; IsA, total area of existing sedimentary islands (ha); AD, average depth (m); Hyd, hydroperiod (percentage of months with water); Leng, shoreline length (m); SDI, shoreline development index.

area (correlated with the flooded surface area and vegetation cover surrounding the lake), the total area of sedimentary islands (correlated with the number of sedimentary islands), shoreline length (correlated with the flooded surface area) and the number of lakes within a 5 km radius (correlated with the lakes in 2 and 10 km radii) were removed from the analysis.

Hierarchical partitioning (HP) analysis, using R^2 as the goodness-of-fit measure, was used to estimate the independent contribution l of each environmental variable to explain species richness. The two groups of variables (local and landscape) were tested separately, and a final model with the significant variables of each group was run again using HP. In all the analyses, a spatial term was incorporated to control for spatial autocorrelation. The spatial term was defined from: $x + y + x^2 + xy + y^2 + x^3 + x^2y + xy^2 + y^3$ (Legendre & Legendre, 1998), using the central UTM coordinates of each lake (López-Iborra, Limiñana, Pavón, & Martínez-Pérez, 2011; López-Pomares, López-Iborra, & Martín-Cantarino, 2015). The significance of the independent contribution of the environmental variables was evaluated by randomization tests based on 999 randomizations (Mac Nally, 2002). Hierarchical partitioning was conducted with the 'hier.part' package (Walsh & Mac Nally, 2003) in the R-program (R Development Core Team, 2016) using the RStudio development environment (RStudio

Team, 2015). The spatial association of the environmental variables was explored using the Mantel test, by constructing a lakes dissimilarity matrix for each environmental variable using Euclidean distance for standardized data, and comparing these matrices with the matrix of distances between sites. The Monte Carlo method with 9999 permutations was used to evaluate significance ($P < 0.05$; Zar, 2010), using the ade4 package (Thioulouse, Chessel, Dolédec, & Olivier, 1997) in the R-program.

3 | RESULTS

Twenty-six wader species were recorded (Table 3). For both seasons, the higher richness values (observed and extrapolated richness) were detected in lakes Camino de Villafranca, Manjavacas, Quero and Veguilla (Table 4). Four of the species are threatened in Europe: curlew sandpiper (*Calidris ferruginea*), black-tailed godwit (*Limosa limosa*), Eurasian curlew (*Numenius arquata*) and northern lapwing (*Vanellus vanellus*). The species that occurred on most lakes were northern lapwing (resident species; 22 lakes), black-winged stilt (*Himantopus himantopus*) and pied avocet (*Recurvirostra avosetta*; breeding species; 21 lakes), and black-tailed godwit (nonbreeding species; 12 lakes) (Table 3).

TABLE 2 List of wetlands studied in the La Mancha Húmeda Biosphere Reserve and their respective conservation status. International designations: Biosphere Reserve (CA: core area; BZ: buffer zone); Ramsar sites (RS); Natura 2000 network (SPA: Special Protection Area; SAC: Special Areas of Conservation). National designations: Protected Area (NR: Natural Reserve; NP: Natural Park)

Lake	Property	Biosphere reserve	Ramsar	Natura 2000	Protected area
Albardiosa	Private	CA		SAC/SPA	NR
Alcahozo	Private/public	CA		SAC/SPA	NR
Altillo Chica	Private/public	CA		SAC/SPA	NR
Altillo Grande	Public	CA		SAC/SPA	NR
Artevi	Private	BZ		SAC/SPA	
Camino de Turleque	Private			SPA	
Camino de Villafranca	Public	CA	RS	SAC/SPA	NR
Campo de Mula	Private			SPA	
Larga de Villacañas	Private/public	CA		SAC/SPA	
Longar	Public	CA		SAC/SPA	NR
Manjavacas	Public	CA	RS	SAC/SPA	NR
Mermejuela	Private	CA		SAC/SPA	
Miguel Esteban	Public	BZ			
Pajares	Public	CA		SAC/SPA	
Pedro Muñoz	Public	CA	RS	SAC/SPA	NR
Peña Hueca	Private	CA		SAC/SPA	NR
Quero	Private/public	CA		SAC/SPA	
Redondilla	Public	CA	RS	SAC	NP ^a
Retamar	Public/private	CA		SAC/SPA	NR
Salicor	Private	CA		SAC/SPA	NR
Tírez	Private	CA		SAC/SPA	NR
Veguilla	Private/public	CA	RS	SAC/SPA	NR
Yeguas	Public	CA	RS	SAC/SPA	NR

^aLake belonging to the Lagunas de Ruidera Natural Park.

Except for the number of lakes within a 2 km radius, no environmental variable showed spatial autocorrelation. In the breeding season, the lake hydroperiod and the number of lakes within the 10 km radius were the only significant variables (apart from spatial term), positively explaining the variability in species richness (Table 5; Figure 2). For the wintering season, maximum flooded surface area was the only significant variable, positively related to species richness, but the number of lakes within a 10 km radius was marginally significant ($P = 0.08$; Table 5; Figure 2). In order to check whether extrapolation could have introduced bias into the data, the analyses considering the same surveys for all the sites identified the same variables in the analyses based on extrapolation (Table S2).

For the breeding period, the final model explained 81% of the deviance, with only hydroperiod contributing significantly to explain species richness (Table 6). For the wintering period, the final model explained 82% of the deviance, with only maximum flooded surface area included as a significant predictor variable (Table 6). In both seasons spatial autocorrelation was important ($I > 60\%$; Table 6). Final models derived from surveys in the common census period added to the aforementioned variables the number of lakes within a 10 km radius (Table S3).

4 | DISCUSSION

Different factors were related to patterns of wader richness in the inland natural lakes of the MHBR, during wintering and breeding

seasons. Local factors were more important than landscape variables for lakes in both periods. Breeding species richness was positively associated with hydroperiod, whereas maximum flooded surface area was associated with increased species richness during the wintering season. Both hydroperiod and flooded surface area were altered by human activities.

Waterbirds are vulnerable to changes in habitat structure during breeding (Hoover, 2009; O'Neal, Heske, & Stafford, 2008; Pino et al., 2000; Sebastián-González & Green, 2013). Variation in the water level of temporary wetlands alters habitat availability, structuring wader communities (Jenkins, Grissom, & Miller, 2003; Vanschoenwinkel et al., 2009). For the breeding period, lakes with extended hydroperiods were richer in wader species than those with shorter hydroperiods (Figure 2). This is particularly important because the hydroperiod of natural lakes in the MHBR region has changed due to anthropogenic causes. In wetlands receiving underground water, the hydroperiod contracts as a result of water extraction for agriculture overexploiting the aquifer (Florín & Montes, 1999). In contrast, some endorheic lakes now receive wastewater input (e.g. Manjavacas, Quero, Veguilla, Pedro Muñoz, Miguel Esteban, Mermejuela, Larga de Villacañas and Longar; Gonçalves et al., 2016), extending the hydroperiod in dry years and providing adequate habitat for foraging and breeding during summer months when the water deficit is high. This leads to some breeding wader populations moving from the wetlands with shortened hydroperiods to lakes receiving wastewater.

TABLE 3 List, migration status (Birdlife International, 2017) and conservation status of native wader species in La Mancha Húmeda Biosphere Reserve (MHBR) in decreasing order of relative occurrence

Species	Common name	Migratory status	Lakes	CS ^b
<i>Vanellus vanellus</i>	Northern lapwing	Resident	22	VU
<i>Himantopus himantopus</i>	Black-winged stilt	Breeding	21	LC
<i>Recurvirostra avosetta</i>	Pied avocet	Breeding	21	LC
<i>Tringa totanus</i>	Common redshank	Resident	14	LC
<i>Charadrius alexandrinus</i>	Kentish plover	Resident	13	LC
<i>Limosa limosa</i> ^a	Black-tailed godwit	Nonbreeding	12	VU
<i>Tringa nebularia</i> ^a	Common greenshank	Nonbreeding	11	LC
<i>Actitis hypoleucos</i>	Common sandpiper	Breeding	10	LC
<i>Calidris alpina</i>	Dunlin	Nonbreeding	10	LC
<i>Calidris canutus</i> ^a	Red knot	Nonbreeding	8	LC
<i>Calidris minuta</i>	Little stint	Nonbreeding	8	LC
<i>Calidris pugnax</i>	Ruff	Nonbreeding	8	LC
<i>Charadrius hiaticula</i> ^a	Common ringed plover	Nonbreeding	8	LC
<i>Tringa erythropus</i>	Spotted redshank	Nonbreeding	8	LC
<i>Calidris alba</i> ^a	Sanderling	Nonbreeding	7	LC
<i>Charadrius dubius</i>	Little ringed plover	Breeding	7	LC
<i>Tringa ochropus</i>	Green sandpiper	Nonbreeding	7	LC
<i>Numenius arquata</i> ^a	Eurasian curlew	Nonbreeding	6	VU
<i>Calidris ferruginea</i>	Curlew sandpiper	Nonbreeding	5	VU
<i>Gallinago gallinago</i>	Common snipe	Nonbreeding	5	LC
<i>Glareola pratincola</i>	Collared pratincole	Breeding	4	LC
<i>Pluvialis squatarola</i> ^a	Grey plover	Nonbreeding	4	LC
<i>Tringa glareola</i>	Wood sandpiper	Nonbreeding	3	LC
<i>Numenius phaeopus</i> ^a	Whimbrel	Nonbreeding	2	LC
<i>Pluvialis apricaria</i>	Eurasian golden plover	Nonbreeding	2	LC
<i>Tringa stagnatilis</i> ^a	Marsh sandpiper	Nonbreeding	1	LC

^aSpecies that according to the maps provided by BirdLife International (2017) are not present in the MHBR.

^bCS: conservation status according to European Red List, available in BirdLife International (2015). Least Concern (LC); Vulnerable (VU).

Wastewater input decreases salinity and increases organic matter in shallow lakes, but with high temperatures in summer it can increase the risk of botulism outbreaks (Vidal et al., 2013), a key factor reducing waterbird populations throughout the world. In the MHBR region, botulism outbreaks have been recorded since 1978 (Vidal et al., 2013), affecting many wader species (Anza, Vidal, Feliu, Crespo, & Mateo, 2016; Minias, Włodarczyk, & Janiszewski, 2016). Specifically, more than 2000 individuals from 19 species died between 1978 and 2008 (Vidal et al., 2013). For black-winged stilt, occurring on many lakes in the study area, mortality rates of 1.8% and 85.3% were estimated in two botulism outbreaks in Navaseca Lake (MHBR region), with variation potentially caused by annual differences in turnover rates (Anza et al., 2016). An extended hydroperiod in summer can also attract other waterbird species (particularly moorhens, gulls and mallards), which may carry *Clostridium botulinum* (Anza et al., 2014; Vidal et al., 2013). Long-term monitoring is essential to assess the potential effects of these disturbances on wader species, especially breeding species in lakes with wastewater input and high contamination.

The hydroperiod was not associated with species richness of waders during the wintering season, possibly because water levels were stable. Maximum flooded surface area was the most important

predictor in winter (Figure 2), probably because of increased habitat. Similarly, pond size was the factor most related to species richness in spring in a group of experimental ponds in Doñana (Sebastián-González & Green, 2013). Guadagnin et al. (2009) also detected a positive relationship between wetland area and waterbird species richness over a year, partly owing to increased microhabitat diversity and individuals in large wetlands. The effect of increased area on waterbird richness is widespread (Brown & Dinsmore, 1986; Rosselli & Stiles, 2012), so it is surprising that in the present study it was only detected in winter. This may have resulted from the strong effect of hydroperiod variation in the lakes studied, overriding the effect of area.

The lakes in the MHBR region have high structural diversity, varying in size, shape and proximity to other wetlands (Doña et al., 2016; Gosálvez, Gil-Delgado, Vives-Ferrándiz, Sánchez, & Florín, 2012; Hera & Villarroja, 2013). Apart from hydroperiod and flooded surface area, lakes within 10 km were related to richness of waders, more intensely during the breeding season and most significantly over the common census period (Table S2). Groups of more than 10 other lakes within this radius had more wader species than lakes that were more isolated. This may reflect daily movements of waders between neighbouring lakes, tracking variation in resource abundance

TABLE 4 Richness observed (Obs) and richness extrapolated (Ext) for the breeding and wintering species for each lake, listed in decreasing order of observed breeding species

Lake	Species richness			
	Breeding		Wintering	
	Obs	Ext	Obs	Ext
Quero	8	8	12	12
Camino de Villafranca	8	8	17	17
Manjavacas	7	7	16	16
Veguilla	7	7	11	11
Salicor	6	6	4	4
Pedro Muñoz	6	6	3	3
Mermejuela	6	6	1	1
Alcahozo	5	5	12	12
Yeguas	5	5	11	11
Artevi	5	6.3	1	1
Longar	4	4	3	4.18
Larga de Villacañas	4	4	2	2
Miguel Esteban	3	3.8	NW	NW
Retamar	3	3.4	NW	NW
Peña Hueca	2	2	3	4.7
Tírez	2	2.8	2	2.4
Altillo Chica	2	2	1	1
Campo de Mula	2	2	1	1
Altillo Grande	1	1	3	4.7
Redondilla	NW	NW	1	1
Pajares	NW	NW	3	3
Camino de Turleque	NW	NW	NW	NW
Albardiosa	NW	NW	NW	NW

NW: lakes without waders.

(Sanzenbacher & Haig, 2002). This effect of isolation on species richness is uncommon (Guadagnin et al., 2009; Sebastián-González & Green, 2013), and perhaps reflects less isolation of wetlands

TABLE 5 Hierarchical partitioning analyses performed to identify the most important variables within each variable group related to the wader species richness during breeding and wintering seasons

	Breeding season					Wintering season				
	%Dev/Sign	I	%I	J	P	%Dev	I	%I	J	P
Local variables	83%					85%				
Flooded surface area		0.02	3.40	0.03	0.63	+	0.15	18.5	0.25	0.03
Vegetation surface area		0.02	3.05	-0.02	0.66		0.01	1.99	0.0007	0.69
Shoreline development index		0.01	2.24	0.009	0.68		0.005	0.61	0.004	0.75
Hydroperiod	+	0.18	21.9	0.16	0.02		0.06	7.43	0.14	0.46
Number of islands		0.009	1.09	-0.004	0.73		0.03	4.14	0.05	0.60
Average depth		0.002	0.32	0.002	0.77		0.08	9.73	0.17	0.34
Spatial term	+	0.56	67.8	0.21	<0.001	+	0.48	57.4	0.32	<0.001
Landscape variables	82%					85%				
Distance from settlement		0.04	5.54	0.02	0.50		0.009	1.11	-0.006	0.69
Number of lakes in 2 km radius		0.02	2.87	-0.008	0.64		0.04	5.39	0.02	0.55
Number of lakes in 10 km radius	+	0.16	20.6	0.14	0.03		0.12	14.6	0.08	0.08
Spatial term	+	0.57	70.9	0.20	<0.001	+	0.66	78.8	0.13	<0.001

%Dev is the percentage deviation explained by the regression model, including all the variables of each group analysed, with sign indicating significant variables, showing the contribution of independent variables (I and %I total), joint (J) and spatial variables.

P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

elsewhere. Other variables related to wader species richness in other studies include average depth (Colwell & Taft, 2000), vegetation cover (Froneman, Mangnall, Little, & Crowe, 2001) and settlement distance (Tavares, Guadagnin, de Moura, Siciliano, & Merico, 2015), but no relationships of these variables were detected, suggesting that their importance may depend on other factors. Other processes, apart from proximity of wetlands, might also explain the importance of spatial dependency.

4.1 | Conservations implications

The record of 26 species, approximately 40% of the wader species of Spain (SEO/Birdlife, 2012), reinforces the importance of the MHBR lakes for aquatic biodiversity in the Iberian Peninsula. Wader richness in the wintering and breeding periods was related to flood surface area and hydroperiod respectively, directly influenced by human activities. Bird conservation strategies in the MHBR have been focused traditionally on waterfowl affected by similar factors, but other wetland characteristics that benefit waterfowl adversely affect waders. The use and management of water resources in this region is affecting the dynamics of the water level in the MHBR wetlands (Fornés et al., 2000) and, consequently, the richness of the wader assemblage. In addition, climate change is likely to aggravate these problems, given projections of decreasing rainfall (Estrela, Pérez-Martin, & Vargas, 2012; Ministerio de Medio Ambiente, 2005). Irrigated agriculture strongly drives the economic development of the region; however, calls to reduce the extraction of underground water have been resisted, severely affecting the wetlands (Esteban & Albiac, 2012). Wastewater has restored flooding in some lakes (Florín & Montes, 1999), but changed the chemical composition of water (García-Ferrer, Camacho, Armengol, Miracle, & Vicente, 2003), invertebrate community (Castillo-Escrivà et al., 2017) and vegetation structure and helophyte cover in the shoreline (Florín & Montes, 1999), with impacts on wader habitat.

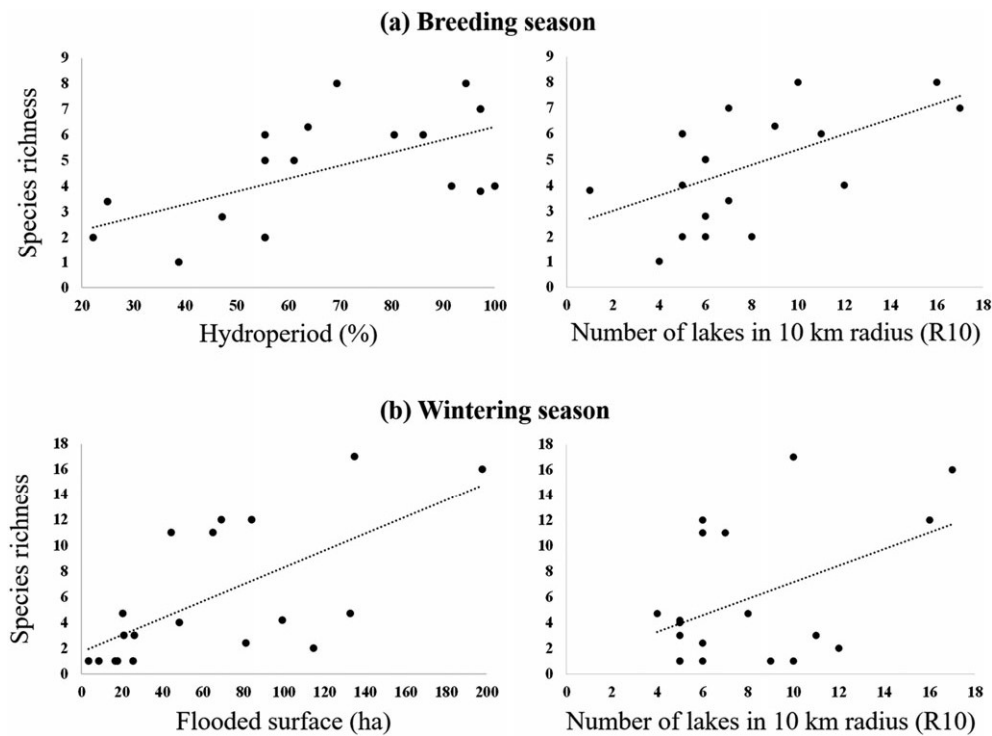


FIGURE 2 The most significant relationships according to contribution (Tables 5 and 6) explaining species richness of waders, with lines of best fit

TABLE 6 Final model of the hierarchical partitioning analyses with the variables of the greatest independent contribution of the two groups of species

	Breeding season					Wintering season				
	%Dev	I	J	%I	P-value	%Dev	I	J	%I	P-value
Final model	81%					82%				
Hydroperiod	+	0.15	0.18	19	0.04	–	–	–	–	–
Flooded surface area		–	–	–	–	+	0.21	0.20	26.2	<0.001
Number of lakes in 10 km radius		0.13	0.17	16.9	0.07	–	–	–	–	–
Spatial term	+	0.52	0.25	64.0	<0.001	+	0.60	0.20	73.7	<0.001

%Dev is the percentage deviation explained by the regression model, including all the variables of each group analysed, with sign indicating significant variables, showing the contribution of independent variables (*I*, %I total), joint (*J*) and spatial variables contributions.

P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

Only four of the 23 lakes studied (Alcahozo, Camino de Villafranca, Miguel Esteban and Pedro Muñoz lakes) are protected by fences. As a consequence, the wetlands are affected by fire, car trails, dogs and garbage, which have often modified the flooded surface and the slope of the lakes, rendering these areas unsuitable for waders. In addition, despite warnings of the negative consequences of using wastewater for wetland restoration (Florin & Montes, 1999), there is no recovery of the original hydroperiod or monitoring of water quality. According to the management plan for the conservation of the Natura 2000 site Humedales de la Mancha (Cubero-Rivera, 2015), the quality of effluent from the sewage treatment systems should be improved by removing mud that has accumulated in wetlands as a consequence of wastewater input. These actions have not been implemented.

In addition to the international designations for site protection, at a national level most of the wetlands studied are classified as Natural Protected Sites, such as Natural Reserves (ecosystems of high

singularity and fragility) and, to a lesser extent, as Natural Parks (sites as important as Natural Reserves, but with higher geomorphological and aesthetic values) (Table 2; Gobierno de España, 2007). These designations should promote the maintenance of environmental quality, but there are few environmental management projects. In addition, the wetlands of the MHBR region are part of private properties or public entities (Table 2). Until recently there was little difference in the legal responsibility between private owners and public entities, but wetlands in private ownership are subject to greater overexploitation owing to the lack of local or regional management measures (Camacho, 2008).

Bird conservation strategies in the MHBR have been traditionally focused on waterfowl affected by similar pressures, but other wetland characteristics that benefit waterfowl have adverse effects on waders. The focus of this study on waders has identified factors that could be managed for wader conservation, although much still needs to be

learned about their complex population dynamics. There are already a range of management strategies prepared that would improve habitats for waders and meet national and international conservation obligations, but they need to be implemented.

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