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Expansion of native wild boar populations is a new threat for semi-arid wetland areas

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ABSTRACT

Wildlife management and conservation requires monitoring of species distribution and population indicators, especially when the unbalanced demographic changes of some species can affect the whole ecosystem functioning. The populations of wild boar (*Sus scrofa*) have, over the past few decades, undergone an expansion around the world, reaching situations of overabundance that can cause serious economic, ecological and health problems. This numerical increase of wild boar and its new spatial invasion can affect certain vulnerable species in sensitive ecological zones, such as the main inland wetland complex in SW Europe.

In this context, we aim to (i) examine the association of wild boar abundance and that of lagomorphs, and waterbird productivity, controlling the possible effects of wild carnivores and other environmental predictors, and (ii) applying a survey method useful for managers to evaluate expected effect of wild boar abundance.

Overall, the presence of wild boar has been detected in 80.8% of the monitored wetlands (n = 26), but a high variation of abundance rates was found. Wild boar abundance negatively associated with the productivity of the entire community of waterbirds, *a priori* highly vulnerable, breeding on shores or islands, both colonially (genus *Gelochelidon, Himantopus, Recurvirostra, Sternula, Glareola, Tringa* and *Phoenicopterus*) or solitary (genus *Anas, Spatula, Mareca, Charadrius, Vanellus, Anser, Ardea, Aythya, Fulica, Netta, Oxyura* and *Tadorna*).

In addition, we evidenced a clear negative association of wild boar and wild rabbit (*Oryctolagus cuniculus*) population abundance in the monitored wetlands. Rabbits are a keystone species in the study area and represent stable prey for many endangered predators.

Our results suggest that potential impacts caused by high wild boar abundance may be already reaching unsustainable levels for some wetlands. Inter-species integrated monitoring is key to address the population management plans of wild boar populations in wetlands and to preserve the most vulnerable species.

1. Introduction

The Eurasian wild boar (*Sus scrofa*) is adapted to a broad range of environmental conditions and nowadays is considered one of the most widely distributed mammals in the world (Baskin & Danell, 2003). Native wild boar populations have not only expanded in natural habitats, but has also successfully occupied human-generated habitats, such as agricultural and *peri*-urban areas, what has supposed a continuous range enlargement during last decades (Apollonio et al., 2010; Massei et al., 2015; Enetwild, 2020). A variety of factors have been related to ongoing wild boar expansion, such as high reproductive rates and adaptability of a species suffering low predation rate, large-scale favourable changes in habitat, legal restrictions on hunting (especially in protected areas), as well as hunting strategies aiming sustainable harvesting (Barrios-Garcia & Ballari, 2012). Therefore, current harvest rates seem to be insufficient to secure numbers low enough to avoid ecological perturbation caused by this species (Massei et al., 2015; Keuling et al., 2016). The impact of over-abundant wild boar on biodiversity conservation and socio-economic interests include sanitary risks to wildlife, livestock and people, vehicle collisions, crop damage, and

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reduction in plant and animal abundance and richness (Massei & Genov, 2004; Barrios-Garcia & Ballari, 2012; Vicente et al., 2013). Besides their direct effects on plant and animal communities (e.g. predation), wild boar can indirectly affect the whole ecosystem functioning through cascading effects caused by modification of vegetal community and habitat structure induced by extended rooting, so it can be considered a relevant ecosystem engineer (Massei & Genov, 2004; Teichman et al., 2013; Carpio et al., 2014). In this sense, wildlife manager interested in developing management policies to mitigate the emerging problem of wild boar expansion requires precise information about the potential ecological effects of wild boar on other species.

More than half of the world́ natural wetlands have been lost in the last century, while the remaining ones have been altered to different degrees due to adverse influences of human-related activities (Fraser & Keddy, 2005). This loss and alteration have been considered a strong driver of alteration in a wide range of avian communities typical of wetland habitats (Czech & Parsons, 2002). Increased nest predation has been suggested as a potentially important additional cause of avian population declines in these ecosystems (Carpio et al., 2016; Fox et al., 2016; MacDonald & Bolton, 2008). In this context, wild boar is also considered a keystone species in wetlands (Dardaillon, 1987; Conway et al., 2005; Giménez-Anaya et al., 2008), and has a high potential to influence on wetland-associated wildlife at population or community level. This is well known in areas where it is an introduced invasive species, such as Australia, USA or the Neotropics (Doupé et al., 2010; Ballari et al., 2015; Engeman et al., 2016), although their effects not always can be considered negative for biodiversity conservation (Arrington et al., 1999; Vanschoenwinkel et al., 2008). Although the wild boar can have significant impacts on different ecosystem components (Barrios-Garcia & Ballari, 2012), little is known regarding the ecological impact of its current densities in native wetland ecosystems (Carpio et al., 2016), except for some species particularly vulnerable to wild boar perturbance (e.g. colonial waterbirds such as pelicans; Crivelli 1996).

In Central Europe, it has been suggested that wild boar may be the main waterbird nest predator in wetlands associated to forest, but not so much in agricultural landscapes (Padyšáková et al., 2010). In Mediterranean areas, wild boar expansion favored by agricultural management (e.g. irrigated corn) may also have negative ecological impact in wetlands near agricultural areas (Herrero et al., 2004; Giménez-Anaya et al., 2008; Rosell et al., 2012), but not always (see Herrero et al., 2006 for riparian habitat). Expanding wild boar populations favored by agricultural management are recently reaching for first time lowland semi-arid areas where wetland communities had not been previously exposed to this ecosystem engineer, that could then be considered an invasive species in the native range too, but information for this kind of wetlands is still scarce (Bouahim et al., 2014). Finally, it is suspected that the expansion of wild boar could also be affecting the abundance of the main small Vertebrate keystone species in Mediterranean ecosystems, the wild rabbit (*Oryctolagus cuniculus*), but this has not been properly evaluated up to now, particularly in agricultural lowlands (Delibes-Mateos et al., 2008).

UNESCÓs Mancha Húmeda Biosphere Reserve (MHBR) is the main group of inland wetlands in the Iberian Peninsula where large populations of waterbirds breed and winter, constituting an international hotspot for biodiversity conservation (Florín & Montes, 1999; Sánchez-Carrillo & Angeler, 2010; Gonçalves et al., 2018). The area holds populations of several species with delicate status at European level, such as Marbled teal (*Marmaronetta angustirostris*), Ferruginous duck (*Aythya nyroca*) or White-headed duck (*Oxyura leucocephala*). At present, it is one of the most threatened wetland systems in Spain and Europe due to human activities, mainly aquifer overexploitation induced by irrigation in agriculture (Martínez-Santos et al., 2008; Cabellos, 2014), a problem particularly serious in semi-arid climates. This wetland assemblage is also one of the most diverse in the world, from deep waters to floodplains or shallow lagoons, from erratically flooded to permanent, from fresh to hypersaline waters and from natural to artificial origin (Florín & Montes, 1999). This ensemble of wetlands provides a unique opportunity for studying wetland-associated wildlife relationships, because (i) it is an area where wild boar abundance was very low in the past and it is still highly variable (from large deforested dryland agricultural areas, mainly unsuitable for this species to highly-suitable areas for wild boar), but where their populations are already in clear expansion, probably facilitated by simultaneous expansion of favourable crops; and (ii) maintain a diverse community of aquatic birds, with internationally relevant breeding populations in wet years.

Effects of wild boar on waterbirds at the population or community levels is still poorly known in sensitive ecological zones, such as wetlands (Herrero et al., 2004; Massei & Genov, 2004). In this context, we intend to (i) examine in detail the potential effect of wild boar on the abundance of lagomorphs and waterbird productivity, controlling the possible effects of wild carnivores and other environmental predictors, and (ii) applying a survey method useful for managers to evaluate expected effect of wild boar abundance, as management recommendations to mitigate this emerging problem.

2. Material and methods

2.1. Study area

This study was conducted in 26 wetlands of Mancha Húmeda Biosphere Reserve at Castilla-La Mancha (central Spain) and nearby areas, distributed over an area of 8000 km^2 in the Upper Guadiana river basin (Fig. 1 and Table S1). The study focused on the "Tablas de Daimiel" National Park (TDNP), one of the most important inland wetlands for waterbirds in Western Europe. "Tablas de Daimiel" were declared as National Park in 1973, included in the Ramsar List in 1982, considered the main core area of the MHBR in 1981, and mentioned as EU Special Protection Area for Birds in 1988. The National Park protects the remaining 1800 ha of a drained floodplain that 60 years ago included ca. 30,000 ha of wetlands (Álvarez-Cobelas & Cirujano, 1996). The climate in this area is cold-temperate semi-arid Mediterranean, with a pronounced dry season, and annual rainfall of 400 to 500 mm with high inter-annual variability. All wetlands studied were between 603 and 670 m above sea level. The selected sample is a good representation of the various kinds of wetlands in the Reserve in terms of depth, size and water traits. During the study year (2015) we found a moderate level of flooding, so several dried wetlands were directly discarded, while most of those with relevant waterbird breeding populations were sampled; see Table S1 and Gonçalves et al., 2018). Many wetlands in the sample correspond to the common kind of endorheic lagoons with irregular flooding and some saline character (Gonçalves et al., 2018). Four of these wetlands (Navaseca, Veguilla, Camino Villafranca and Miguel Esteban) receive treated wastewater inputs from treatment plants of nearby towns. Historically, they had marked variability in flooding levels, since water supplies to these lagoons were originally regulated by irregular rainfall and surface runoff. Regular supply of fresh water discharged from wastewater treatment plants into these lagoons has altered their natural hydrological or saline character. One of them is Navaseca, a temporary endorreic lagoon currently converted to a highly eutrophized artificial wetland with permanent water, the closest one to TDNP (6.5 km away; Fig. 1).

3. Waterbird monitoring

Waterbird populations were sampled by fixed points close to wetlands trying to visually cover all water table at adequate distances for identification of birds, so the number of observations points was adjusted to the size of each wetland (Supporting Information S1, see additional details in Laguna et al., 2016). We counted all adult waterbirds observed and their chicks when present (fixed stations; n = 90) in the 26 monitored wetlands. Each wetland was sampled once at peak

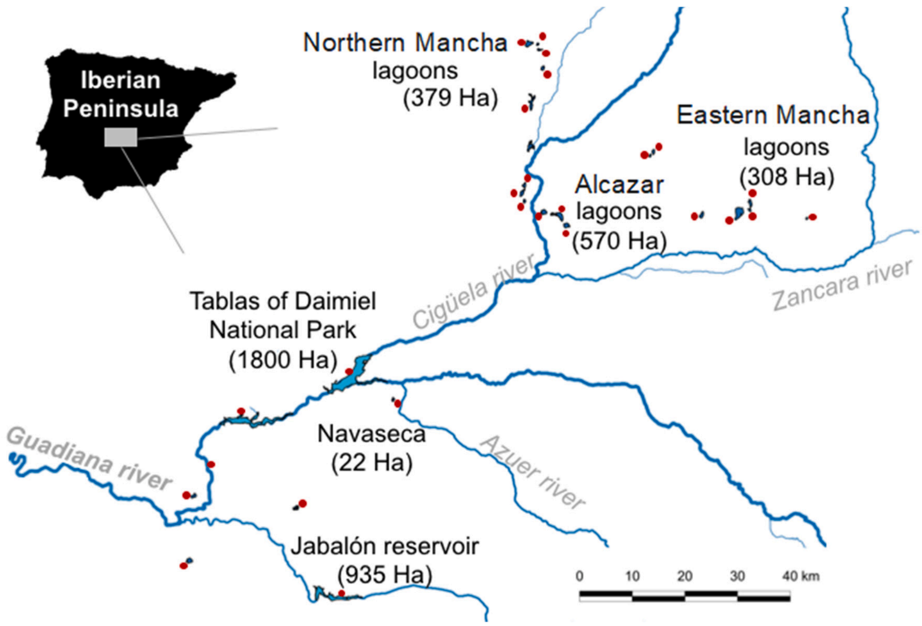

Fig. 1. Map of monitored wetlands (n = 26) in “Mancha Húmeda” (Spain), within the upper Guadiana river basis. This is considered the most important inland wetland complex for waterbirds in South-West Europe and the most important representation of semi-arid wetlands in western Mediterranean area.

breeding time to maximize the probability of finding chicks (June-July), always by two of the authors (XP and CZ).

Given the main objective of this work, to know the potential impact of wild boar on the reproductive success or abundance of waterbirds, we have classified waterbird species according to their potential vulnerability to predation, depending on aggregation of individuals and typical nesting site as a proxy to the degree of accessibility to wild boar (Table 1). When a species could use several types of breeding sites, we have included it in the category that would be *a priori* less sensitive to predation, i.e. with a conservative criterion (Table 1).

Table 1
Classification of monitored waterbird species according to nesting-site preferences and aggregation pattern during nesting.

Group	Subgroup	Species
Semi- or colonial. Nesting on ground with scarce water or plant cover (C)	Colonial. Shore and island ground nesting without plant cover (C1)	*Gelochelidon nilotica* *Himantopus himantopus* *Recurvirostra avosetta* *Sternula albifrons*
	Colonial. Nesting in shore or shallow water (C2)	*Glareola pratincola* *Tringa totanus*
	Colonial, shallow water with abundant mud (C3)	*Phoenicopterus roseus*
Solitary. Ground nesting in wetland edge (S)		*Spatula clypeata* *Anas crecca* *Anas plathyrhynchos* *Mareca strepera* *Charadrius alexandrinus* *Charadrius dubius* *Vanellus vanellus*
Solitary. Nest on water with thick plant cover or cavities in wetland edge (W)		*Spatula querquedula* *Anser anser* *Ardea purpurea* *Aythya ferina* *Aythia nyroca* *Fulica atra* *Netta rufina* *Oxyura leucocephala* *Tadorna tadorna*
Floating vegetation-nesting in deep water (F)		*Chlidonias niger* *Chlidonias hybrida* *Chroicocephalus ridibundus* *Podiceps cristatus* *Podiceps nigricollis* *Tachybaptus ruficollis*

4. Abundance estimation of mammals

Abundance of mammal species was estimated in all studied wetlands through the presence frequency of faecal droppings on walked transects (n = 54; Acevedo et al., 2007). Two types of 4 km transects counts were performed on every wetland (two radial and one along the perimeter of flooded area), during March-July 2016. Overall, the design of transects was initially stratified by habitat type which was characterized every 200 m, to sample all available habitats near wetlands according to their extension. Each 4 km transect count consisted of 40 segments of 100 m length and 1 m width, divided into 10 sectors of 10 m length. Sign frequency was defined as the average number of 10 m sectors containing droppings of each studied species: wild boar, red fox (*Vulpes vulpes*), European wild rabbit (*Oryctolagus cuniculus*) and Iberian hare (*Lepus granatensis*) per 100 m transect. Based on sign frequencies, a frequency-based indirect index (FBII) was calculated according to Acevedo et al. (2007):

$$\mathrm{FBII} = \frac{1}{n}\sum_{i=1}^{n} S_i$$

where S_i is the number of sign-positive sectors in the ith 100 m transect (i.e., S_i varies between 0 and 10) and n is the number of transects considered (i.e., $n = 40$ for the total analysis). In addition, for the case of wild boar, we also obtained the abundance index per transect by counting presence of soil rooting and footprints (Carpio et al., 2016). This is the same equation described previously, considering the number of positive sectors (S_i) to the presence of soil rooting and footprints

5. Environmental predictors

Previous studies have described that wetland size, water depth and salinity are important variables determining both the structure of waterbird communities and breeding success of them (Taft et al., 2002). Wetland size has been considered as the average flooded area during the study period, while water depth and salinity were classified in three categories (<1m, 1–2 m, >2m deep; and freshwater, mid-salinity and high-salinity water, respectively; Table S1).

In addition, three environmental variables about hydrogeological traits of wetlands, water quality and conservation status were incorporated as potential predictors of wetland-associated wildlife species (Ma et al., 2010; Table S1). First, the hydrogeological classification of wetland origin included fluvial lagoon systems, endorheic/aquifer supplied, and mixed/other (volcanic, reservoir, karstic water bodies). Water quality was categorized in two levels: wetlands without treated sewage effluents and wetlands with presence of these pollution effluents (from partially eutrophic to hypertrophic). Conservation status of the wetlands was described according to De Groot et al. (2007) and Laguna et al. (2011) in three categories (conserved, altered and greatly altered/intervened), which are equivalent to the conservation degree assessment of Habitat Directive (European Commission, 2015).

6. Modelling approach

The variables depicting waterbird populations were total population (chicks and adults pooled) and productivity (chicks/adults ratio) of the (i) whole waterbird population, (ii) waterbird population without F group (floating vegetation-nesting in deep water), (iii) and of the 4 species groups in Table 1 and S2. Thus, each observation point in the wetlands was characterized by six environmental predictors, four mammal abundance rates and 12 response variables about waterbird community.

We implemented the same methodology for all models explaining spatial variation in waterbird response variables. A preliminary exploration of the data was performed to obtain a better understanding of their characteristics, and to avoid violating assumptions of analytical procedures (Zuur et al., 2010). This exploration mainly included an examination of variable distribution, outlier detection, and collinearity diagnosis among candidate predictors. Spearman's correlation tests were used to assess the correlation between explanatory variables (variables with rho > 0.6 were removed). In addition, as some predictors had multiple degrees of freedom, multi-collinear variables were excluded using a variance inflation factor (VIF) coefficient > 2.5 threshold cut-off value (Zuur et al., 2010). The unit of interest for modelling purposes was observation point which number varied between 1 and 7 per wetland, depending on size of the water table and visibility from each point. Therefore, we used generalized linear mixed models (GLMM) where random factor was the wetland identity, while wetland size was controlled as weight variable. For the monitoring data (abundance and productivity), each model was tested assuming normal (Gaussian) and gamma error. Model selection based on an information-theoretic framework was used to test combinations of explanatory variables with ecological significance based on our predictions (Burnham & Anderson, 2002). This approach included the main effects of variable structure that could potentially affect the response variables as a null comparable model among different responses. Standard model checks (homoscedasticity and normality assumptions of residuals) were tested with 'lme4' R package (Bates et al., 2014), concluding that best results were obtained assuming normal error. Model residuals were also examined and tested for spatial autocorrelation using the Moran's I to detect spatial structures (Diniz-Filho et al., 2003). Raw data were not transformed, and real abundance rates were used throughout the analyses. The 'Coefplot2' package was used to plot the model results (Bolker & Su, 2011).

7. Results

Overall, the presence of wild boar has been detected in 80.8% of the monitored wetlands, but with high variation in abundance (Fig. 2). Iberian hare abundance was comparatively low in areas where wild boar was abundant (Spearman's correlation r = -0.31, p = 0.02), and a stronger effect on the same direction was found for rabbit populations (Spearman's correlation r = -0.49, $p < 0.001$; Fig. 3). However, no significant relationships were found between red fox abundance and lagomorph populations (Fig. 3).

Regarding effects on waterbirds, Fig. 2 shows the distribution of overall waterbird population throughout sampled wetlands. Overall, we monitored 29 species, from which 23 (79.4%) nested in the areas more vulnerable to wild boar perturbation, while 6 species corresponded to F category, expected to be less affected (Table 1). The full model structure for overall waterbird abundance included wetland origin, water quality and water depth, as well as wild boar and carnivore abundance. Conservation status and salinity were rejected as explanatory variables (VIF value > 2.5), and wetland size was included in all models as weight variable. A general model including all waterbird species revealed no effects of any predictor in abundance nor productivity. However, when the same analysis was performed without the F group -*a priori* less vulnerable to nest predation-, a significant reduction of productivity was found in wetlands with high wild boar abundance (z = -0.25, $p < 0.01$; Fig. 4; Table S2). In this sense, wild boar abundance has been negatively related to the productivity of the entire community of waterbirds, *a priori* highly vulnerable, breeding on shores or islands, both colonially or isolated (Table 1).

Model results for each waterbird group in Table 1 are detailed in Table S2. Summarizing, wild boar abundance negatively associated with the productivity of species groups C, S and W ($z = -0.32$, $p < 0.05$; $z = -0.22$, $p < 0.01$; $z = -0.17$, $p < 0.05$, respectively), but no F. However, no association with waterbird population was observed for estimated fox abundance. Other effects observed in the specific models included the affinity of C group to the endorheic/aquifer base lagoons ($z = 1409.01$, $p < 0.01$), the negative effect of pollution effluents on abundance of S group (z = -1150.34, p < 0.05) and the high abundance of F group in deep wetlands (z = 541.13, p < 0.05).

8. Discussion

Our results show that wild boar is already present inside or near most wetlands of MHBR (81%), while just some decades ago its presence was unknown or sporadic in most of them. This evidences the rising impact of this species. Wild boar abundance was highest in the most important wetland in the area, TDNP, where recreative hunting is prohibited (Palomo et al., 2014) and only limited population regulation implemented by the park authorities is allowed. On average, 65 wild boar are captured per year in the National Park, which only entails an extraction rate of 3.6 animals per square kilometre (NP Director, Carlos Ruiz, pers. comm.). Therefore, a large area with no hunting and large reedbed cover likely plays a crucial role as "refuge area" for wild boar (Amici et al., 2012). This, in conjunction with proximity to a small forested ridge with high wild boar density and peripheral favourable crops (particularly maize), allows high reproductive success, which may explain this exceptionally high abundance (Rosell et al., 2012). Furthermore, wild boar abundance in TDNP (FBII 0.47) was similar to high density of large game estates in the study region (FBII 0.39–0.12; Acevedo et al., 2007).

We found a negative relationship between the abundance of wild boar and lagomorphs (rabbit and hare), more pronounced in the case of rabbits. This is of serious concern given that the rabbit is a keystone species in Mediterranean ecosystems, owing to its prey condition for at least 29 different predators, among them 17 raptors and 9 carnivores, which feed on rabbits (Delibes-Mateos et al., 2008). This relationship is consistent with previous studies carried out in other habitats in Iberia (Cabezas-Díaz, Virgós, Mangas, & Lozano 2011, Carpio et al., 2014).

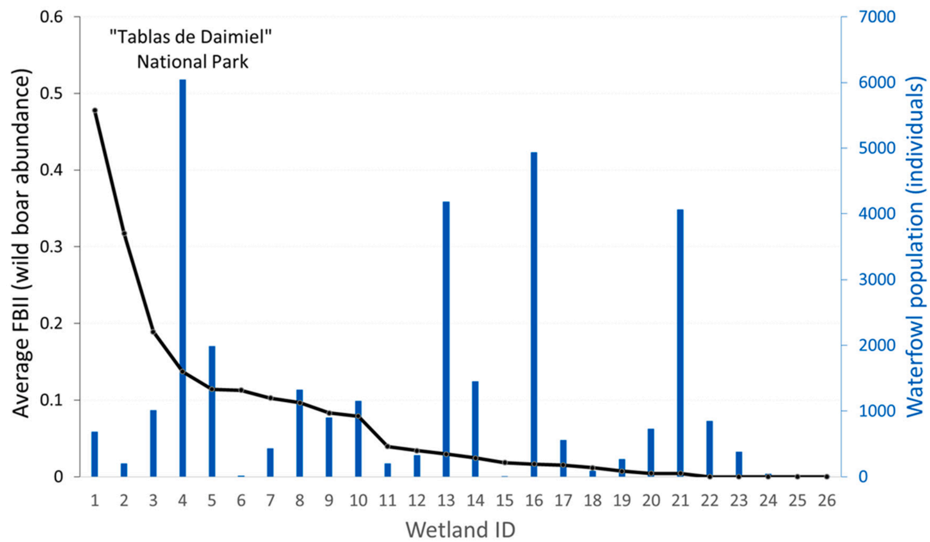

Fig. 2. Distribution of wild boar abundance rates (black solid line; estimated as the frequency-based indirect index, FBII; Acevedo et al., 2007) and total estimated waterbird population (blue bars; observed individuals) throughout the monitored wetlands. Numbers in X axis refer to wetland. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

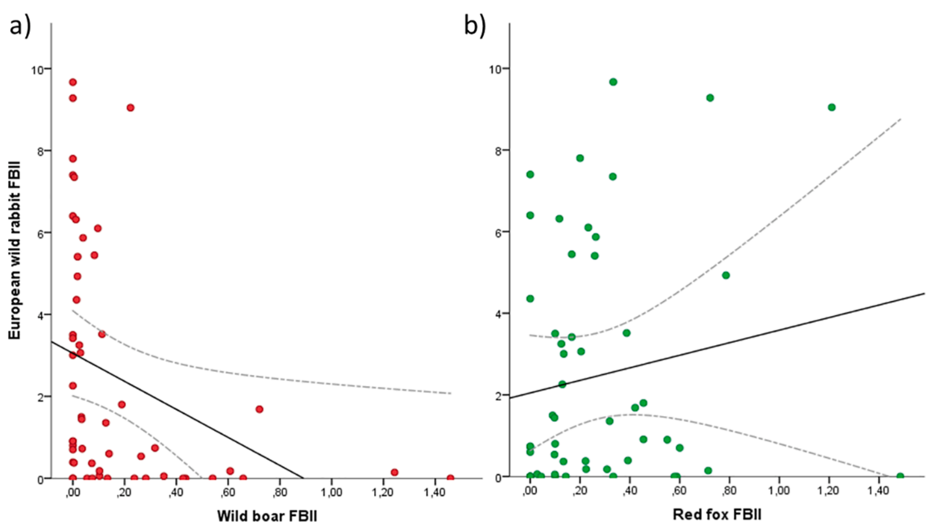

Fig. 3. Relationships among the frequency-based indirect abundance index (FBII; Acevedo et al., 2007) of wild rabbit against (a) wild boar FBII and (b) red fox FBII in the surrounding areas of the sampled wetlands. Dashed grey lines show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Wild boar activity reduces herbaceous coverage and leguminosae proportion in pastures, causing a marked increase in the total percentage of soil disturbed as a result of rooting (Carpio et al., 2014), and they may also have an effect through direct predation of young rabbits and warren perturbation (Hummel et al., 2017). These potential negative effects therefore can induce a 'competitor pit effect' that may limit rabbit numbers (Cabezas-Díaz et al., 2011). By contrast, in the case of the fox, no negative relationship was found, which can be explained by the fact that generalist predators are attracted to the areas with the greatest abundance of lagomorphs (Calvete & Estrada, 2004), which concentrate their foraging efforts on higher rabbit abundance areas (Viñuela et al., 1994).

According to our results, wild boar abundance negatively associated with the productivity of all groups of waterbirds (Table 1), except F group (floating vegetation-nesting in deep water), which can be due to nests of this group being less accessible to wild boar as deep water provides protection against terrestrial predators (Picman, Milks, & Leptich, 1993; Hoover, 2006) (but not so much for aerial predators, see Djelailia et al., 2018). However, for the rest of the groups (C, W and S), wild boar abundance negatively associated with productivity, probably because these groups nest in areas more accessible to terrestrial predators (Purger & Mészáros, 2006) and frequently used by wild boar when present, as reedbeeds and edges of water bodies. In this case, dense vegetation can be the main protection against predation (Fouzari et al., 2015). Wild boar rooting activity also affects the height and cover of vegetation, potentially increasing the risk of nest predation (Roda & Roda, 2016). In addition, wild boar disturbance includes grazing of the vegetation and stirring of sediments, causing bioturbation which could affect stonewort (*Chara* sp.) meadows. In this sense, wild boar bury (and consume) a proportion of the seeds found on the surface (Bonis & Lepart, 1994), and secondarily increase water turbidity and eutrophication, attenuating light needed for aquatic macrophyte growth (similar to *Cyprinus carpio* effect; Laguna et al., 2016). Stonewort meadows are a key element of this aquatic ecosystems, as well as a major food source for herbivorous waterbirds (such as *Fulica atra* or *Mareca strepera*) or diving ducks (such as *Netta rufina* or *Aythya ferina)* (van den Berg et al., 1998;

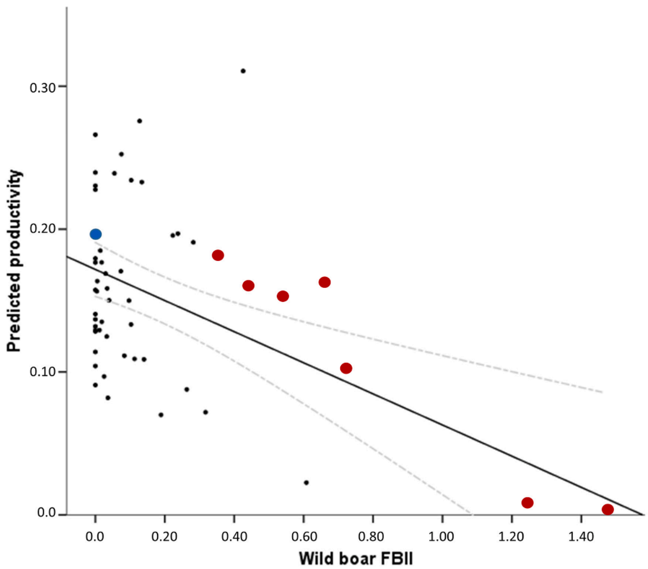

Fig. 4. Relationship between the productivity of the entire community of waterbirds predicted by the model (except F group, species with floating vegetation-nesting in deep water) and frequency-based indirect abundance index (FBII; Acevedo et al., 2007) of wild boar in the surrounding areas of the same wetlands. Blue dot shows Navaseca lagoon, while red dots represent the lagoons in "Tablas de Daimiel" National Park. Dashed grey lines show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Noordhuis et al., 2002). Therefore, submerged vegetation is essential in supporting waterbird communities, and this is true not only for herbivorous species (Laguna et al., 2016).

Low waterbird breeding success was particularly worrying at TDNP, where the highest abundance of wild boar was found. Interestingly, in the nearest wetland to the park (Navaseca Lagoon; Fig. 4), much smaller, with higher human perturbation and affected by sewage discharges, but where wild boar presence was not recorded, waterbirds had a much better breeding success. This contrast at low spatial scale suggest that wild boar presence may be the most relevant single factor affecting waterbird breeding success in these wetlands.

By contrast, the abundance of wild boar did not associate with the abundance of waterbirds that may be more dependent on environmental variables and characteristics of the wetland (Sherry et al., 2015). For example, group C abundance was higher in endorheic wetlands (a closed drainage basin that normally retains water and allows no outflow to other external bodies of water), as expected for species typical of shallow lakes and ponds (Sebastián-González & Green, 2014). On the other hand, the abundance of the S group was positively associated with the presence of endorheic basins and negatively with pollution effluents. Group W includes a more ecologically heterogeneous set of species, with no clear relationship between abundance and environmental predictors. Finally, group F includes those species characterised by nesting in floating vegetation and nesting in deep water, which determines the positive effect of the variable water deep (>2m deep) and independence with respect to wild boar abundance.

9. Management implications

The main result of this study are the negative relationships found between the abundance of wild boar and the abundance of lagomorphs or productivity of most waterbirds (except group F), the latter particularly marked in the most important wetland, TDNP. Our results support that National Park authorities should intensify management of wild boar impact in the area (van Beeck Calkoen et al., 2020) and that regional authorities in charge of biodiversity conservation should seriously consider long-term monitoring of wild boar abundance and impact in wetlands, as well as applying new management where necessary. The proposed wild boar index (FBII, Figs. 3 and 4), previously tested in other habitats, could be a good indicator of wild boar impact to be used by managers to evaluate wild boar disturbance and applying management when necessary, or even allowing early intervention on this emerging problem before waterbird productivity may suffer important decline in a given lagoon. Our results tentatively suggest that FBII values higher than 0.2–0.3 indicate wild boar abundance rates seriously reducing both rabbit abundance and waterbird productivity, but a longer survey would necessary to fine-tune this preliminary threshold to different environmental conditions or wetland typology, within an adaptive management program combining yearly surveys and population control or mitigation measures. Mancha Húmeda Biosphere reserve, seriously threatened by aquifer overexploitation, low water quality and invasive species (Florín & Montes, 1999, Laguna et al., 2016), must add wild boar abundance as an emerging relevant threat, too. Our study also highlights the possible need of management against disturbance by wild boar in other wetlands of the reserve, either by population control, habitat management or protection of nesting areas. Beyond the specific case, harmonized monitoring of wild boar, and by extension, wild ungulates, their impacts, and other wildlife (i.e. migratory birds) is required to implement coordinated wildlife management and conservation at European level (Enetwild, 2018).

Additional research is needed to clarify which of the multiple potential disturbances caused by wild boar is more relevant explaining the strong effect of its presence in semi-arid wetlands on the productivity of waterbirds (direct predation of nest, disturbance in nesting sites, ecological alteration caused by rooting and/or use of reedbeds as refuge), what may help to guide future management of the problem.

10. Author's contributions

JAB, CG and JV conceived the ideas and designed methodology; JAB, MB, XP, CZ and JV collected the data; JAB, AC and JV analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107563.

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