Agricultural policies against invasive species generate contrasting outcomes for climate change mitigation and biodiversity conservation

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Abstract

Direct consequences of biological invasions on biodiversity and the environment have been largely documented. Yet collateral indirect effects mediated by changes in agri-environmental policies aimed at combating invasions remain little explored. Here we assessed the effects of recent changes in water management in rice farming, which are aimed at buffering the impact of the invasive apple snail (*Pomacea maculata,* Lamarck), on greenhouse gas emissions and diversity of waterbird communities. We used observational data from a two-year field monitoring (2015-2016) performed at the Ebro Delta regional scale. We found that drying rice fields reduced methane emission rates by 82% (2015) and 51% (2016), thereby, the contribution of rice farming to climate change. However, there was a marked reduction (75 % in 2015 and 57 % in 2016) in waterbird diversity and abundance in dry fields compared with flooded fields, thus suggesting that post-invasion policies might hinder biodiversity conservation. Our results highlight the need for accounting for potential collateral effects during the policy decision-making process to design efficient agricultural management plans that lessen undesirable agri-environmental outcomes.

Keywords Rice; Apple snail; greenhouse gases; waterbirds; Ebro Delta; wetlands

Introduction

Biological invasions are considered a major driver of global change that entail marked environmental and socio-economic costs worldwide [1–3]. Only in the European Union, economic losses in agriculture associated with the introduction of invasive species amounted to US$ 36 billion during the 1960-2020 period [4]. Direct effects of invasive species on crop production are mostly mediated by weeds, pests, and plant pathogens [5]. Strategies for reducing pressure of invasive pests include chemical and biological fight, but also changes in management practices which are promoted through agri-environmental policies (AEP) [3]. Environmental outcomes resulting from AEPs may be controversial as new remedial actions may trigger collateral effects on biodiversity and on biogeochemical cycles. For example, changes on agricultural management at large spatial scales may modify habitat availability for native non-target species [6] as well as the capacity of agroecosystems for carbon sequestration or greenhouse gas emissions [7]. Yet these potential side effects of AEPs on multiple global environmental issues are rarely incorporated by policy makers when designing invasive species management plans.

Rice (*Oryza sativa*, L) is a globally important semi-aquatic crop with important implications for global food security, climate change, and biodiversity conservation [8]. Firstly, flooded rice fields (i.e., rice is grown under flooded conditions) occupy around 12 % of the global cultivated area (~164 million hectares) and is the principal source of food for one third of the world's population [9]. Rice farming is also recognized as one of the main agricultural sources of greenhouse gas emissions, as decomposition of organic matter under anaerobic soil conditions (i.e., flooding conditions) promotes high rates of methane (CH_4) emission [10–12]. Finally, rice agroecosystems are biodiversity hotspots with especial relevance for waterbird conservation as flooding fields act as unique artificial wetlands that provide feeding and breeding habitat to a broad range of species worldwide [13–17]. Strategies for reducing crop damage caused by aquatic invasive pests such as the apple snail (*Pomacea maculata*, Lamarck) include modifications of the flooding dynamics at the landscape scale (e.g., long periods of field drying), which are subsidized by regional governments through specific AEPs [18,19]. Importantly, changes in water management could entail side effects leading to positive outcomes for greenhouse gas emissions but negative outcomes for waterbird conservation. Yet, these collateral effects of management actions against invasive species remain largely underexplored and, therefore, are not usually considered by policy makers.

In this study, we used the rice agroecosystem of the Ebro Delta (NE Spain) as a case study to explore the potential side effects of the application of regional policies to control the invasive apple snail (i.e., post-harvest drying of rice fields) on methane emissions and the diversity of avian communities. Before the accidental introduction of the apple snail in winter 2009/2010, rice farmers were subsidized through AEPs for maintaining rice fields flooded during the post-harvest season (i.e., winter) as the region is one of the three most important wetlands in the Western Europe in terms of waterbird diversity. As a result, more than 65 % of the agricultural surface remained flooded during winter providing large amounts of habitat for wintering waterbirds [18]. However, the large scale winter flooding also acted as an important source of methane emission in the region [11,12]. To help at controlling apple snail populations, which cause serious rice yield losses, post-invasion AES-policies did not include the payment to rice farmers for flooding rice fields, entailing a marked reduction in the flooding surface at the Ebro Delta scale (Figure 1). Here, to evaluate the potential side effects of water management changes on methane emission and avian diversity, we used an observational approach based on two-year field monitoring. We specifically characterized methane emission rates and bird diversity throughout the post-harvest season considering two contrasting scenarios in terms of flooding dynamics (flooded vs. dry). We hypothesized that the management policies against the apple snail have an indirect positive effect on climate change mitigation (i.e., reduction of methane emission rates), as draining of rice fields introduce aerobic soil conditions that inhibits methane emissions. On the other hand, we expected a negative effect on biodiversity conservation (i.e., reduction of species richness and evenness of communities) as drying fields would provide low suitable habitat for waterbird species. We additionally tested whether the hypothesized negative effect of field drying on waterbird diversity could be compensated by an increase of non-waterbirds diversity.

Material and Methods

Study system

The study was performed in the Ebro Delta, a 320-km^2 area located in Northeast Spain (Catalonia, Figure 1). The Ebro Delta is considered one of the most important wetlands in the Northwest Mediterranean. Around 25 % of the region (ca. 8000 ha) is protected as a Natural Park and is included in the Natura 2000 network, in the Ramsar convention and as part of Terres de l'Ebre Biosphere Reserve [16,20]. On the other hand, about 65 % of the territory (21,125 ha) is dominated by an agricultural matrix aimed at growing rice during the spring-summer season (from May to September) [21]. Because rice is cultivated under flooded conditions, this agricultural matrix act as an artificial wetland during the rice growing season. In addition, the Ebro Delta acts as a wintering ground for more than 250,000 waterbird individuals annually foraging in the area (seeds, aquatic plants and invertebrates and fishes) [22]. Yet the availability of foraging habitat for wintering birds largely depends on the water management of rice fields during the post-harvest period (i.e., November to February). Until 2010 post-harvest flooding (of *ca.* 63

% of the overall agricultural surface) was promoted as an environment-friendly practice supported by the Agri-Environmental Schemes of the European Commission. Implementation through regional agricultural policies included financial support to rice farmers and was aimed at providing wintering waterbird habitat, but also at promoting other agronomic benefits (e.g., straw decomposition) and duck hunting grounds [23–26]. However, the accidental introduction of the invasive apple snail (*P. maculata*, Lamarck) in winter 2009/2010 [27,28] dramatically changed this scenario. Apple snail, which is included among the World's worst invasive species (IUCN) because its huge impact on rice yield worldwide [27,29], rapidly spread throughout the Ebro Delta. As response, the post-invasion regional policy (PDR 2014-2020) did not incorporate the AEP's winter flooding as a funded agricultural practice, thus promoting the interruption of flooding during winter. This helped to slow down the invasion process and reduce the agricultural impact during the first stages of the pest invasion process [30], yet it drastically reduced progressively the amount of flooded surface at the regional scale (pre-invasion period, 63 % *vs.* overall post-invasion period, 55 % *vs*. the last 6 years, 35 %; Figure 1). Given that most waterbird species surveyed use disproportionally rice fields, natural wetlands (approx. 2500 Ha) and/or salt mines (approx. 1000 Ha) as foraging habitats [22], post-harvest field drying reduced the suitable habitat at the delta regional scale from approximately 16,800 Ha (pre-invasion period) to 10,890 Ha (the last 6 years). It is important to note, however, that despite the application of post-harvest field drying during more than a decade, the apple snail has already occupied all the north-side of the delta and it is currently expanding in a scattered way throughout the southern side [30].

Characterization of methane emission rates

Methane emission rates (mg · m^{-2} · h^{-1}) were estimated in 24 rice fields (*n* = 15 in 2015; *n* = 9 in 2016; Figure 1), averaging 2.15 ± 0.08 (mean ± SD) hectares. Fields were selected to represent two contrasting scenarios from the point of view of the flooding state: dry fields (i.e., water layer height = 0 cm in more than 95 % of the field surface) *versus* flooded fields (i.e., water layer height > 0 cm in more than 95 % of the field surface) (Figure S1). Yet it is worth noting that flooding state of a given field can change across the post-harvest season, thus the flooding state of the studied fields was characterized in each fortnightly survey. Sampling locations were widely distributed across the Ebro Delta to capture environmental variability in terms of biotic and abiotic conditions at the regional scale (Figure 1).

Only methane was considered as previous studies showed that emissions of additional greenhouse gases (i.e., nitrous oxide and carbon dioxide) are negligible during the post-harvest season in our study system [12,31]. Three sampling points were established for each rice field, which were randomly distributed across the field. The height of the water layer was also measured in the same sampling points. Gas sampling was conducted on a monthly basis from October to December, using non-steady state gas chambers [11,32]. The characteristics of the chambers as well as the procedure for chamber deployment and field sampling plan are detailed in Martínez-Eixarch *et al.* [11]. In brief, the chambers, were made of polyvinylchloride (PVC) structure covered by transparent plastic and they were equipped with a thermometer to monitor temperature within the chamber in each gas sample extraction. To avoid soil disturbance during gas sampling, blocks were installed in the field to support wooden boards to access the chamber. All the rice fields were randomly sampled within the same day and consistently from 10:00 am to 3:00 pm to minimize variability derived from the daily emission variation [33]. During the sampling procedure, each gas sample was transferred overpressured to pre-evacuated 12.5 mL vials (Labco Ltd., Buckinghamsire, UK) and sent to laboratory. Methane (CH_4) concentration was determined using a Thermo Trace 2000 (Thermo Finnigan Scientific, USA) gas chromatograph equipped with a flame ionization detector (GC-FID). The calibration of the gas chromatograph was carried out using a CH_4 standard in nitrogen provided by Carburos Metalicos S.A. (Spain). The emission rates of methane were obtained from the change of concentration of the respective gas in chambers over the 30-min sampling period in each chamber. The emission rate was estimated by the slope of the linear regression between gas concentration and sampling time. The increase of temperature in the headspace of the chamber was considered to correct methane concentration of each sample.

Characterization of avian communities

Characterization of avian communities was conducted during the post-harvest rice season (i.e., winter, November to January) in 2015 and 2016. We selected a total of 27 rice fields ($n = 15$ in 2015; $n = 12$ in 2016); i.e., the same 24 fields selected for estimating greenhouse gas emissions plus three additional fields in 2016. Diurnal bird surveys were performed every two weeks, with the first sampling date (i.e., 11th November 2015 and 7th November 2016) coinciding with the third fortnight after harvesting ($n = 6$ fortnightly surveys per year for two years, totaling 12 fortnightly surveys). With the help of binoculars and a telescope all recorded individuals during 15-min censuses were identified at the species level by expert ornithologists of the research group (A. Bertolero & S. Rivaes) [34]. In addition, each species was categorized as a waterbird or a non-waterbird species. Waterbirds included gulls (Fam. Laridae), herons and ibis (Fam. Ardeidae and Threskiornithidae) and waders (Orders Charadriiformes and Gruiformes), whereas the non-waterbirds included songbirds (Order Passeriformes), raptors (Order Falconiformes) and an assortment of a few surveyed species that cannot be included in any of the previous categories ("*others*" functional group) [35] (Table S1). The functional groups are composed by phylogenetically related species (same family or order) with shared common functional traits (e.g., body size or foraging behaviour); except for the "*others*" group (see 36, 37 for similar agrupations)

Field and landscape characterization

In every single visit the following habitat characteristics were characterized at the field scale as they are expected to influence bird diversity: *i*) two semi-quantitative measures indicating the proportion of the field surface with water and with straw residues (i.e., 0 %, 5 %, 25 %, 50 %, 75 % and 100 % for each measure), *ii*) the mean height of the water layer (average of three random points for each field), and *iii*) whether the rice straw were or were not incorporated into the soil. In order to control for the landscape influence on avian diversity patterns, we also characterized the composition of the surrounding habitat for each focal field (1-km buffer). We used the *QGIS* software and the land-use shape layer (10-m resolution) provided by the regional government of Catalonia (https://territori.gencat.cat/; year 2017). Specifically, we estimated the surface (ha) occupied by the following habitat features: *i*) rice matrix, *ii*) agricultural matrix (no rice), *iii*) natural wetlands, *iv*) urban areas, and *v*) other habitat features that included shrublands and coastal habitat.

Data analysis

To evaluate the effect of water management during the post-harvest season on methane emission rates we applied a generalized linear mixed-effect modelling approach (GLMM). The model included the rate of methane emission as the response variable and the interaction between the flooding state (i.e., dry *vs.* flooded) and sampling year as the main fixed factors ($n = 216$ observations). We included this interaction to test for temporal consistency in the effects of water management on methane rates. The initial temperature in the chamber and the height of the water layer were included as covariates. Finally, because we established three repeated measures (sampling units) per plot and fortnightly survey, we included a nested random factor with fortnightly survey nested within plot identity. Because data distribution was markedly left-skewed with clustered zero values (i.e., no methane emission), we used a tweedie distribution with a *log* link function [38].

To evaluate the impact of changes of winter flooding patterns on waterbird diversity, we firstly estimated both species richness and Hill Evenness (i.e., a modified Simpson index or q_2) for each sampled rice field across fortnightly surveys by using the iNext R package (Hill numbers) [39–41]. Both components are complementary and summarize properly the biodiversity profiles of sampled rice fields. Richness indicates the total number of species detected whereas Hill Evenness is interpreted as the effective number of dominant species in the community [39,41]. We then applied two GLMMs for modelling species richness ($n = 162$ observations) and Hill Evenness ($n = 162$ observations), respectively. Both models included the interactions between flooding state and sampling year and between flooding state and fortnightly survey as main fixed factors, whereas local (i.e., field size, height of the water layer, and the incorporation of straw residues) and landscapes variables (i.e., amount of rice matrix in the 1-km buffer) were included as covariates. Given the high correlation detected among the rest of local and landscape variables, they were not included in the model to avoid potential multicollinearity issues (Figure S2). Both models included the plot identity as a random factor whereas a negative binomial and a gaussian distribution were used for the species richness and evenness model, respectively. All abovementioned analyses were repeated by including not only the diversity of waterbirds, but also the diversity of the whole avian community (i.e., waterbirds + raptors + songbirds + "*others*").

In order to assess how flooding patterns affected the abundance of the different functional groups of birds we also applied a GLMM by using the overall abundance (i.e., the sum of abundances across fortnightly surveys) of each species in each flooding state as the response variable (*n* = 208 observations). The interaction between flooding state and the functional group, and the interaction between flooding state and the sampling year were included as fixed factors. Then, we incorporated the identity of the species as a random factor and used a negative binomial distribution of errors. Finally, to test if, as hypothesized, reduced avian diversity in dry fields is compensated by an increase of avian biomass, we estimated the overall biomass of bird communities for each plot and fortnightly survey. We obtained the weight (Kg) for each surveyed species from the AVONET database [42], and then multiplied by their abundances. We then applied a GLMM by using the total biomass of birds for each fortnightly survey and plot as the response variable (*n* = 162 observations). The plot surface and the interactions between flooding state and year and flooding state and fortnightly survey were incorporated as fixed factors. Avian biomass was square root transformed to improve model fitness. Finally, the identity of the plot was incorporated as a random factor and a tweedie distribution with a *log* link function was specified. We used *R software* (v4.1.2) [43] and the *glmmTMB R* package to perform all the GLMMs [44]. In addition, the *DHARMa* package was used to check for potential patterns in model residuals by using both a visual inspection of residual plots and the formal tests provided by the library [45]. We also used *emmeans* for computing contrast between factor levels [46], and *tydiverse* for both data management and visualization [47].

Results

We found evidence that, during the post-harvest rice period, field drying reduces methane emission rate when compared to flooded fields ($\chi^2 = 5.4$, $P = 0.019$; Figure 2, Table S2). This pattern was consistent across years as shown by the non-significant interaction between the year of sampling and flooding state of fields ($\chi^2 = 0.9$, $P = 0.340$). Specifically, percentual reduction in methane emission rates in dry fields when compared to flooded fields was 82 % in 2015 (flooded fields = 4.5 ± 1.8 $mg \cdot m^{-2} \cdot h^{-1}$ *vs.* dry fields = 0.8 ± 0.5) and 51 % in 2016 (2.4 ± 1.1 $mg \cdot m^{-2} \cdot h^{-1}$ *vs.* 1.2 ± 0.9). In addition, we found statistical evidence that the height of the water layer had a significant negative effect on methane emission rates ($\chi^2 = 5.4$, $P = 0.018$), whereas temperature had a strong positive effect ($\chi^2 = 16.2$, $P < 0.001$).

Our results showed very strong evidence of reduced waterbird richness in dried fields when compared to flooded fields ($\chi^2 = 26.8$, $P < 0.001$, Table S3) during the post-harvest season. This pattern was consistent between years as evidenced by the non-significant effect of the sampling year × flooding state interaction ($\chi^2 = 2.3$, $P = 0.132$). On average, avian richness was reduced by *ca*. 75 % in 2015 (flooded fields = 2.5 ± 0.5 *vs.* dry fields = 0.6 ± 0.1) and by 57 % in 2016 (2.1 ± 0.4 *vs.* 0.9 ± 0.2). The GLMM output showed a statistically significant interaction between fortnightly survey and flooding state ($\chi^2 = 15.8$, $P < 0.001$), showing a positive relationship between avian richness and fortnightly survey for flooded fields ($t = 2.7$, $P = 0.008$) but a negative relationship for dry fields ($t = -2.9$, $P = 0.004$) (Figure S3). Finally, there was a strong positive effect of field size on waterbird richness ($\chi^2 = 18.5$ $P < 0.001$), and the extent of the rice matrix around focal fields did not influence it ($\chi^2 = 0.1$, $P = 0.779$). The results were quite consistent when we included also the non-waterbird species in the analysis (i.e., raptors, songbirds and "*others*" groups) (Figure 3, Table S4).

We consistently found that species evenness (i.e., Hill Evenness) was also lower in dry fields than in flooded fields for both years (χ^2 = 34.5 $P < 0.001$, Table S3). Specifically, we observed a reduction of evenness by 71 % (flooded fields = 1.7 ± 0.2 *vs.* dry fields = 0.5 ± 0.1) in 2015 and by 49 % in 2016 (1.6 ± 0.2 *vs.* 0.8 ± 0.2). The sampling year x flooding state interaction was not statistically significant (χ^2 = 2.7, $P = 0.097$), suggesting that the patterns were consistent for both years. Fortnightly survey and flooding state showed a statistically significant interaction mirroring the results for species richness (χ^2 = 13.8, $P < 0.001$), i.e., a positive relationship in flooded fields (t = 3.2, $P = 0.002$) and a negative trend in dry fields (t = -1.9, $P = 0.050$) (Figure S3). Field size also positively influenced species evenness (χ^2 = 8.0, $P = 0.005$), whereas the amount of rice matrix showed no evidence of influence (χ^2 = 0.001, $P = 0.972$). The results remained consistent when the additional non-waterbird species were included in the GLMM (Figure 3, Table S4).

The abundance of birds in rice fields was highly influenced by water dynamics (χ^2 = 6.1, $P = 0.014$; Table S5), yet its effect differed among groups as shown by the bird group × flooding state interaction (χ^2 = 16.9, $P = 0.004$). Specifically, we found a negative effect of field drying in herons and ibis (t = -2.4, $P = 0.018$) and waders (t = -3.7, $P < 0.001$), while no effect was detected for gulls (t = -1.2, $P = 0.228$), songbirds (t = 1.2, $P = 0.238$), raptors (t = -0.7, $P = 0.493$) and the "*others*" functional group (t = 0.09, $P = 0.92$) (Figure 4). The pattern was consistent for both years as shown by the non-significant interaction between flooding state and sampling year (χ^2 = 3.0, $P = 0.081$). Finally, overall biomass of avian communities was also influenced by the flooding state of fields (χ^2 = 16.9, $P < 0.001$; Table S6), showing higher values for flooded than for dry fields. Despite this trend tended to be consistent between years (i.e., higher avian biomass in flooded than in dry fields), it was only statistically significant for the first year as shown by the significant interaction between flooding state and year ($\chi^2 = 13.5$, $P < 0.001$) (Figure S4).

Discussion

Direct environmental consequences of biological invasions have been largely documented [1–3], yet the collateral effects of invasive species -via changes in AEPs- on important environmental issues such as climate change and biodiversity conservation remain unexplored. Here we show that large scale changes in the dynamics of field flooding promoted to control the invasive apple snail in the Ebro Delta entails contrasting outcomes in terms of climate change mitigation and conservation of bird diversity. Specifically, field drying during the post-harvest rice season largely slow down methane emission rates across the post-harvest season, thus reducing the contribution of rice farming to climate change. On the other hand, we found a markedly reduction of waterbird diversity and abundance in dry fields when compared to flooded fields, suggesting that post-invasion policies might hinder conservation of biodiversity in the studied region.

Rice farming contributes 48 % of cropland greenhouse gas emissions globally [48], mainly because of its unique flooding system. In the studied rice-growing region, two thirds of methane emissions occur during the flooded post-harvest season [12], yet our results show that field drying drastically reduced mean emission rates by 82 % and 51 % in 2015 and 2016, respectively (Figure 2). Alternate wetting and dryings [49] has been already documented as an efficient strategy to reduce methane emission during the growing season as aerobic conditions inhibit methanogenic archaea activity [50]. Our results suggest that implementing field drying in the fallow season can be an efficient strategy to counteract the contribution of rice farming to methane emissions which is aligned with Belenguer-Manzanedo *et al.* [31]. Despite the significant effect of flooding regime on methane emissions, it was remarkable the presence of zero emissions under flooded conditions contrasting with some emissions detected in dry fields (Figure 2). The cluster of zero methane emissions under flooded conditions mainly corresponds to the late autumn or winter period [11,31], when soil temperature in rice fields is below the optimal range (15 – 30ºC) for methanogenesis [51]. This is coherent with the strong positive effect of temperature on methane emission rates found in our study, which is explained by an increased activity of methanogenic microbial activity during warm days [11,52,53]. One the other hand, methane emissions in dry fields can be explained by patches of saturated soil during the drying of the fields, where despite the absence of a layer of water, soil moisture preserves anaerobic conditions and thus methanogenesis. As previously reported in Martínez-Eixarch *et al.* [11] our results indicate also a negative effect of the water layer height on methane emissions rates, most likely resulting from a process of methanotrophy in the water column [11]. This suggests that maintaining a high layer of water might help in reducing the emissions of methane associated to rice fields that remain flooded during the post-harvest season.

The positive effect of AEP-mediated field drying on climate change mitigation markedly contrasted with the negative outcome in terms of waterbird conservation. Feeding habitat provided by flooded rice agroecosystems during the post-harvest season have been documented to play a crucial role in attracting a broad range of migratory and resident waterbird species during the non-breeding season (18, but see ref 19). Our results show that flooded fields attracted more waterbird species (75 % in 2015 and 57 % in 2016) than dry fields, most likely as a consequence of higher availability of feeding resources [54]. Similarly, species evenness (i.e., Hill Evenness) was also higher in flooded fields, indicating a higher number of common abundant species than in dry fields

(Figure 3). Reduced diversity (i.e., richness and evenness) resulted not only from the loss of low tolerant species to field drying, but also from a consistent decrease of abundance of almost all individual species of herons and ibis, gulls and waders (Figure 4). Reduced diversity of waterbird communities in dry fields was not compensated by an increment of non-waterbird species, as differences between flooded and dry fields remained quite similar when we included songbirds, raptors and other low-abundant species in our analysis (Figure 3). In fact, contrarily to the observed pattern for waterbirds, the abundance of non-waterbird species was quite similar in both dry and flooded fields (Figure 4). Reduced diversity was neither compensated by an increment of biomass of drought tolerant species, but instead overall biomass was also reduced in dry fields (Figure S4).

By analyzing the long-term International Waterbird Censuses (IWC) database, Pernollet *et al.* [18] also showed a positive effect of the post-harvest flooding AEPs at increasing the attractiveness of European rice fields for wintering waterbirds. A recent re-analysis of this database for the Ebro Delta has reopened the debate, as they did not find evidence on a positive effect of post-harvest flooding on waterbird population trends neither a negative effect after its cessation [19]. An explanation for this result could be that even a small amount of remaining flooded rice fields plus the natural wetlands are enough to buffer the temporal loss of habitat, at least for some waterbird species. Other large scale factors such as climate change [55,56] or habitat disturbances at the breeding grounds [57,58] may be also shaping waterbird communities beyond the Ebro Delta. However, another potential explanation might rely in the fact that the abovementioned study [19] did not consider interannual variation in the proportion of flooded surface at the regional scale, which can largely vary across years (Figure 1). In addition, they included in the analysis several species that use rice fields anecdotally (e.g., Pied avocet, Kentish plover, etc.), whereas they did not include other species that are intimately linked to rice fields (e.g., Glossy ibis, European golden plover, etc.) [22]. Therefore, ignoring interannual variation in flooding patterns and potential differences among species with contrasting dependence on rice fields could be masking the negative effect of the cessation of the post-harvest flooding on overall waterbird population trends. Our results may be even more relevant from a waterbird conservation perspective if we note that the reduction of flooded habitats is also happening in other important wintering areas in Southern Europe, such as the Doñana National Park [59]. Finally, the reduction of flooded surface is expected to affect to different groups of organisms that are intimately linked to the water layer of rice fields (from microorganisms to vertebrates), especially those with low tolerance to drying periods [60] and/or low dispersal capacity [61] (e.g. tadpoles, larval stages of macroinvertebrates, fishes or crayfishes).

Globalization of human activities is entailing a continuous flux of invasive species worldwide, promoting changes in agri-environmental policies to buffer the economic and environmental impacts in the invaded regions [62]. Here we show that these changes in AEPs may shift the contribution of the invaded agrosystems to other global environmental issues such as climate change and biodiversity conservation. Our results highlight the need for gathering basic information on the ecology of worst invasive species (e.g., colonization patterns, reproductive biology) to better anticipate their response to habitat management and the effectiveness of large scale management practices to control or eradicate their populations. In the Ebro Delta, after a decade of post-harvest field drying, the apple snail has colonized the whole northern side of the delta and is colonizing the southern side in a scattered way [30], questioning the effectiveness of this practice to control the snail populations. Alternative practices such as washing fields with marine water or the use of molluscicides have also been used to control snail populations, however they are not exempt from problems due to the collateral effects they may entail on crop yield (soil salinization) or in communities of non-target organisms, respectively [30].

Our study emphasizes the importance to account for potential collateral effects during the policy-making process to design efficient agricultural management plans that enable to minimize undesirable agri-environmental outcomes. For example, regional plans against invasive species should incorporate the landscape scale and consider to sectorize and/or fallow the application of agricultural practices (e.g., post-harvest drying of rice fields) according to different criteria such as pressure of invasive species on agriculture, conservation importance for birds or mitigation potential of greenhouse gas emissions. We acknowledge this is a more knowledge and resource demanding strategy than homogenizing and simplifying management plans, yet it is also expected to better reduce potential trade-offs among different agri-environmental issues. This especially important in complex agroecosystems such as rice systems of the Ebro Delta, which are especially vulnerable to invasive species while play an important role as food producers, greenhouse gasses sources, and biodiversity hotspots.

Data accessibility

The datasets generated and analysed during the current study are available in the figshare repository [63].

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Author contributions

NPM, MME and CA conceived and designed this study. AB, CA, MME, and SR were responsible for field and labwork. NPM analyzed data with contribution of JPGV and LG. NPM wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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Figures

Figure 1. Study system. *Upper panel:* Flooding patterns promoted by Agri-Environmental Policies (AEPs) in the Ebro Delta to control populations of the invasive apple snail (*P. maculata*). Bars show the temporal distribution of flooded surface (%) relative to total rice surface in the Ebro Delta during the post-harvest rice seasons in both the pre-invasion and post-invasion period. Flooding data was obtained from Pernollet *et al.* (2015; period 2002-2012) and from the Generalitat de Catalunya (period 2016-2021)[1]. The framed bars with a dashed line indicates the sampling years of this study. *Lower panel:* Spatial and temporal distribution of sampling locations in the Ebro Delta. Circles represent rice fields where greenhouse gas emissions and avian diversity were quantified, whereas squares indicate fields where only avian diversity was characterized.

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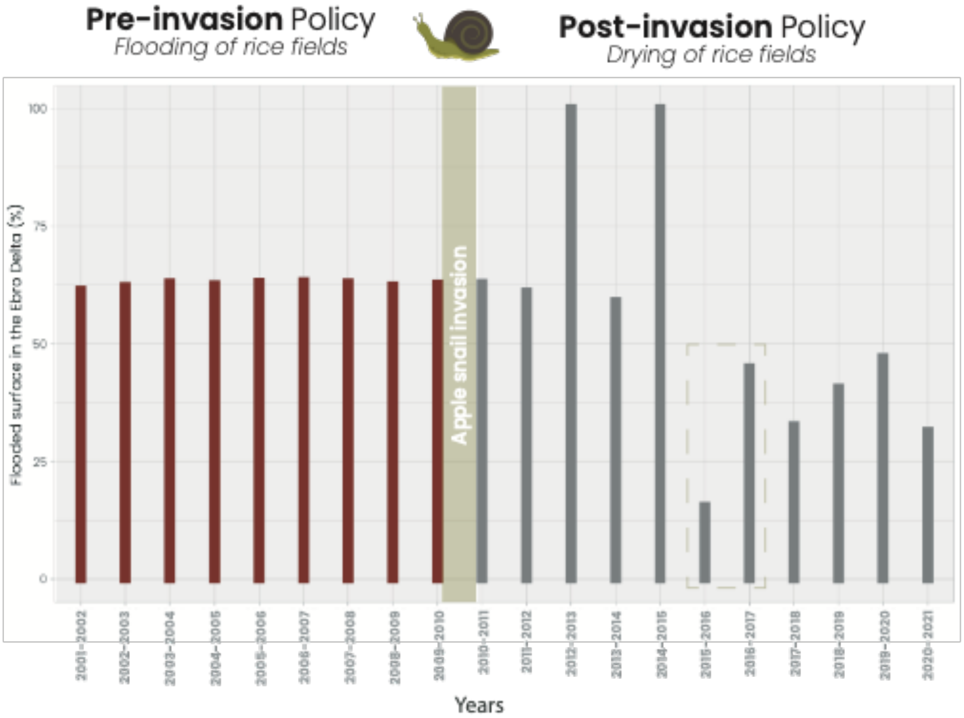
[1] https://govern.cat/govern/docs/2021/02/22/13/01/c10b629b-e1fd-4f35-8a7e-ecb7d145398e.pdf


Pre-invasion Policy
Flooding of rice fields
Post-invasion Policy
Drying of rice fields
Flooded surface in the Ebro Delta (%)
100
75
50
25
0
Apple snail invasion
2001-2002
2002-2003
2003-2004
2004-2005
2005-2006
2006-2007
2007-2008
2008-2009
2009-2010
2010-2011
2011-2012
2012-2013
2013-2014
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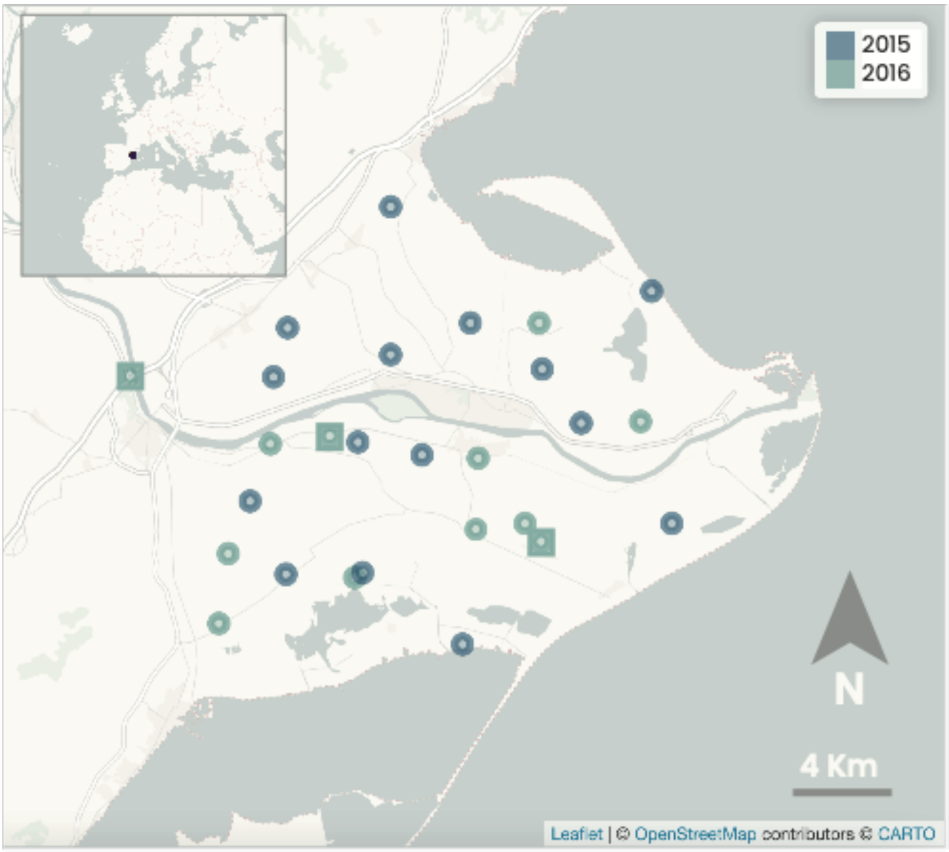
2015-2016
2016-2017
2017-2018
2018-2019
2019-2020
2020-2021
Years


2015
2016
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Leaflet | © OpenStreetMap contributors © CARTO

Figure 2. Methane emission rates (mg · m^{-2} · h^{-1}) in dry (red points; 2015: $n = 63$; 2016: $n = 21$) and flooded rice fields (blue points; 2015: $n = 72$; 2016: $n = 60$) in the Ebro Delta. Small semi-transparent points indicate observed methane emission rate for each field and fortnightly survey. Large solid points and error bars indicate the estimated emission rate and the standard errors provided by the GLMM, respectively. Note the log-scaled y-axis.

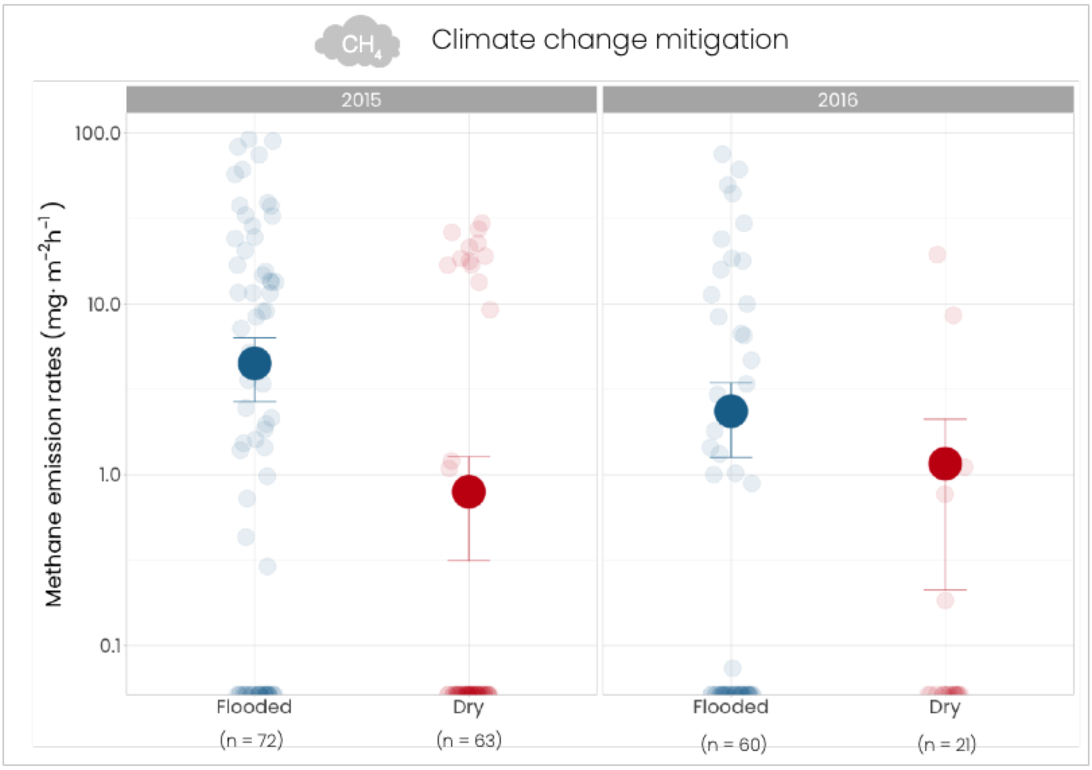


Figure 3. Avian diversity patterns in dry (2015: *n* = 57; 2016: *n*= 31) and flooded rice fields (2015: *n* = 33; 2016: *n*= 41) in the Ebro Delta. Left panels (a and b) show diversity patterns for waterbird communities, whereas the right panels (c and d) show patterns for the whole avian communities (i.e., also including songbirds, raptors, and the "*others*" functional groups). Small semi-transparent points indicate observed richness (panel a and c) and Hill Evenness (panel b and d) for each field and fortnightly survey. Large solid points and error bars indicate the estimated means and the standard errors provided by the GLMMs, respectively.

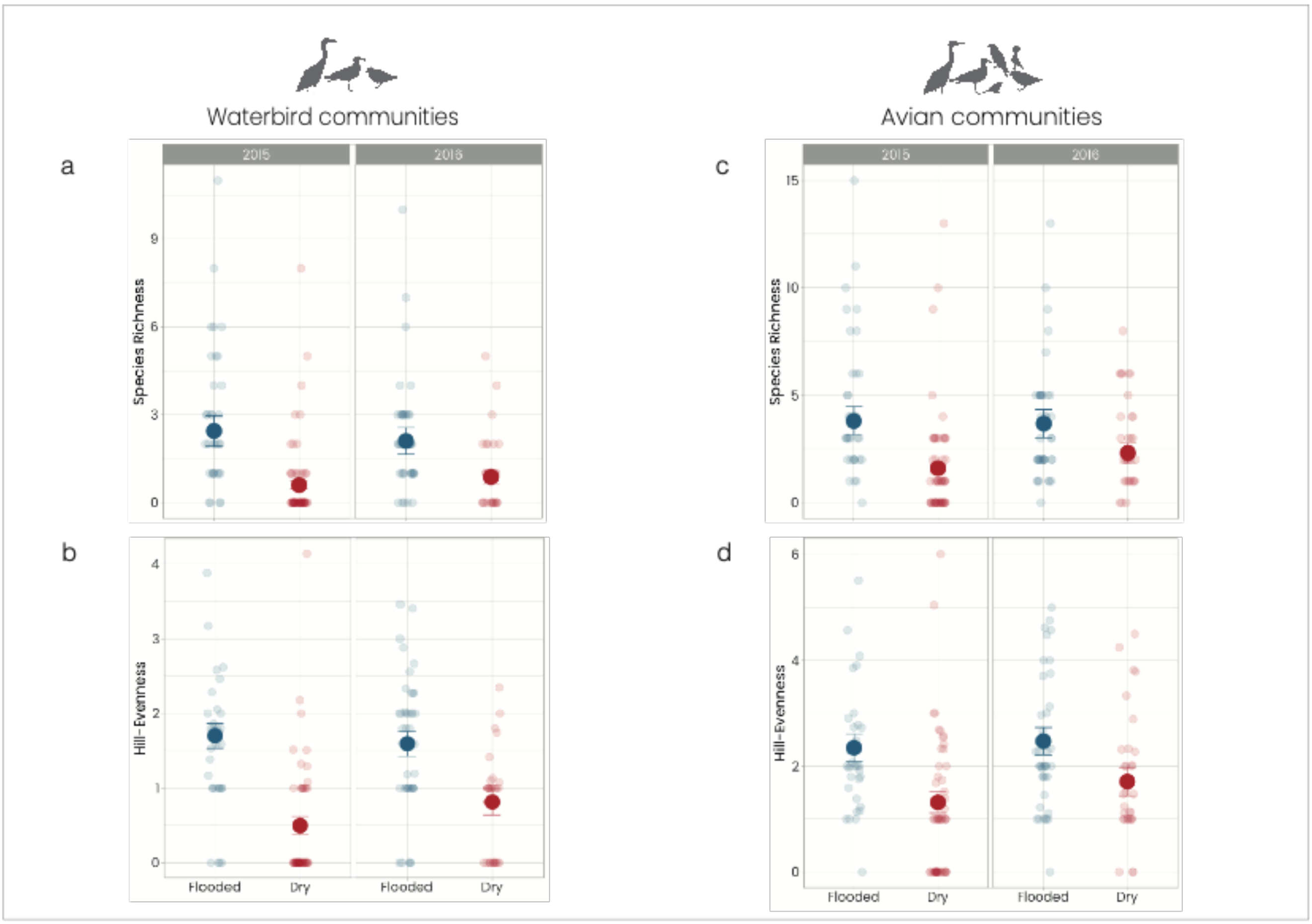
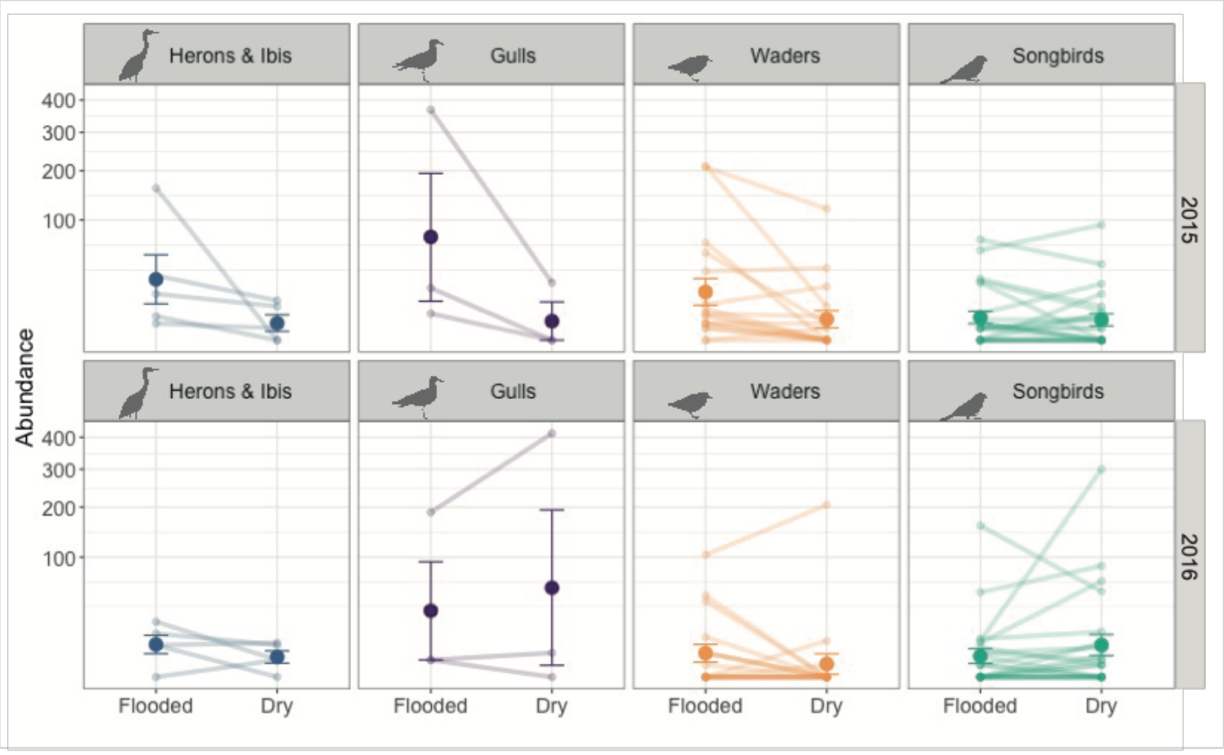


Figure 4. Abundance of the different functional groups of birds in flooded and dry rice fields. Semitransparent points and lines indicate the accumulated abundance at the end of the post-harvest season for each bird species of different functional groups. Solid points and error bars indicate averaged accumulated abundance (± SE) across species. Note that raptors and the *"others"* functional groups were not included as they were very few abundant. The y-axis is square root scaled.



Supplementary Material for

Agricultural policies against invasive species generate contrasting outcomes for climate change mitigation and biodiversity conservation

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Table S1. List of surveyed species and the accumulated abundance (± SD) per plot in both flooded and dry fields. Note that species abundance for both years (2015 and 2016) were pooled.

Species	**Functional group**	**Flooded (mean ± SD)**	**Dry (mean ± SD)**
Ardea cinerea	Herons & Ibis	0.378 ± 0.771	0.17 ± 0.485
Bubulcus ibis	Herons & Ibis	0.027 ± 0.163	0.034 ± 0.183
Ardea alba	Herons & Ibis	0.149 ± 0.395	0
Egretta garzetta	Herons & Ibis	0.676 ± 1.283	0.148 ± 0.704
Plegadis falcinellus	Herons & Ibis	2.27 ± 12.643	0.091 ± 0.853
Chroicocephalus ridibundus	Gulls	7.514 ± 22.466	4.955 ± 37.278
Larus fuscus	Gulls	0.095 ± 0.501	0
Larus michahellis	Gulls	0.284 ± 1.419	0.045 ± 0.336
Actitis hypoleucos	Waders	0.027 ± 0.163	0.034 ± 0.237
Calidris alba	Waders	0.014 ± 0.116	0
Calidris alpina	Waders	0.946 ± 7.331	0
Calidris minuta	Waders	2.851 ± 24.411	0.091 ± 0.853
Calidris pugnax	Waders	0.176 ± 1.012	0
Charadrius alexandrinus	Waders	0	0.011 ± 0.107
Charadrius hiaticula	Waders	0.122 ± 1.046	0.33 ± 2.328
Gallinago gallinago	Waders	1.257 ± 5.147	0.023 ± 0.15
Numenius arquata	Waders	0.054 ± 0.327	0
Pluvialis apricaria	Waders	1.068 ± 5.369	0.409 ± 3.731
Tringa erythropus	Waders	0.014 ± 0.116	0
Tringa glareola	Waders	0.108 ± 0.632	0
Tringa nebularia	Waders	0.122 ± 0.495	0
Tringa ochropus	Waders	0.122 ± 0.522	0.045 ± 0.209
Tringa totanus	Waders	0.027 ± 0.232	0
Vanellus vanellus	Waders	4.23 ± 8.071	3.693 ± 11.546
Alcedo atthis	Others	0	0.023 ± 0.15
Phalacrocorax carbo	Others	0.027 ± 0.163	0
Circus aeruginosus	Raptors	0.041 ± 0.199	0.011 ± 0.107
Falco tinnunculus	Raptors	0.027 ± 0.163	0.011 ± 0.107
Anthus pratensis	Songbirds	0.203 ± 0.641	0.409 ± 1.035
Linaria cannabina	Songbirds	0	0.091 ± 0.6
Carduelis carduelis	Songbirds	0.081 ± 0.517	0.011 ± 0.107
Chloris chloris	Songbirds	0.027 ± 0.232	0.011 ± 0.107
Cisticola juncidis	Songbirds	0.027 ± 0.163	0
Emberiza schoeniclus	Songbirds	0.027 ± 0.163	0
Erithacus rubecula	Songbirds	0.014 ± 0.116	0
Fringilla coelebs	Songbirds	0.459 ± 3.15	0.818 ± 5.804
Luscinia svecica	Songbirds	0.014 ± 0.116	0
Motacilla alba	Songbirds	1.622 ± 3.148	1.432 ± 3.043
Motacilla cinerea	Songbirds	0.014 ± 0.116	0.023 ± 0.15
Motacilla flava	Songbirds	0.014 ± 0.116	0.011 ± 0.107
Passer domesticus	Songbirds	0.378 ± 1.856	0.136 ± 0.571
Phoenicurus ochruros	Songbirds	0.068 ± 0.253	0.068 ± 0.254
Phylloscopus collybita	Songbirds	0.027 ± 0.163	0.114 ± 0.385
Pica pica	Songbirds	0.081 ± 0.321	0.034 ± 0.183
Saxicola torquatus	Songbirds	0.014 ± 0.116	0.045 ± 0.209
Serinus serinus	Songbirds	0	0.057 ± 0.533
Sturnus sp.	Songbirds	0.432 ± 2.365	3.409 ± 31.98
Sturnus unicolor	Songbirds	0	0.182 ± 1.601
Sturnus vulgaris	Songbirds	2.905 ± 16.183	1.625 ± 6.349

Table S2. Outputs of the GLMMs applied for modelling methane emission rates. Values in bold indicate statistically significant effects. The reference levels for the categorical variables are *Flooded* (Flooding state) and *2015* (Year).

Methane rate	**Variable**	χ^2	***p-value***
	Flooding state	5.4	**0.019**
	Year	0.7	0.393
	Water level	5.4	**0.018**
	Temperature	16.2	***<0.001***
	Flooding state × Year	0.9	0.340

Table S3. Outputs of the GLMMs applied for modelling species richness and Hill Evenness of waterbird communities (i.e., excluding non-waterbird species). Values in bold indicate statistically significant effects. The reference levels for the categorical variables are *Flooded* (Flooding state) and *2015* (Year).

Species richness	**Variable**	χ^2	***p-value***
	Flooding state	26.8	***<0.001***
	Year	0.05	0.823
	Fortnightly survey	0.06	0.812
	Field size	18.5	***<0.001***
	Rice matrix surface	0.08	0.779
	Flooding state × Year	2.3	0.132
	Flooding state × Fortnightly survey	15.8	***<0.001***
Hill Evenness			
	Flooding state	34.5	***<0.001***
	Year	0.55	0.458
	Fortnightly survey	0.28	0.595
	Field size	8.00	***0.005***
	Rice matrix surface	0.001	0.972
	Flooding state × Year	2.75	0.097
	Flooding state × Fortnightly survey	13.8	***<0.001***

Table S4. Outputs of the GLMMs applied for modelling species richness and Hill Evenness of whole bird communities (i.e., including waterbirds and non-waterbird species). Values in bold indicate statistically significant effects. The reference levels for the categorical variables are *Flooded* (Flooding state) and *2015* (Year).

Species richness	**Variable**	χ^2	***p-value***
	Flooding state	15.1	***<0.001***
	Year	0.6	0.44
	Fortnightly survey	1.8	0.18
	Field size	18.3	***<0.001***
	Rice matrix surface	3.4	0.06
	Flooding state × Year	1.9	0.17
	Flooding state × Fortnightly survey	20.5	***<0.001***
Hill Evenness			
	Flooding state	11.5	***<0.001***
	Year	1.0	0.32
	Fortnightly survey	1.3	0.25
	Field size	6,0	***0.01***
	Rice matrix surface	2.9	0.09
	Flooding state ×Year	0.4	0.53
	Flooding state × Fortnightly survey	11.8	***<0.001***

Table S5. Outputs of the GLMMs applied for modelling differences in abundance of the different functional groups of birds. Values in bold indicate statistically significant effects. The reference levels for the categorical variables are *Flooded* (Flooding state) and *2015* (Year).

Avian abundance	**Variable**	χ^2	***p-value***
	Flooding state	6.10	**0.014**
	Functional group	0.05	0.355
	Year	0.06	**0.031**
	Flooding state × Group	16.99	**0.004**
	Flooding state × Year	3.04	0.081

Table S6. Outputs of the GLMMs applied for modelling differences in avian biomass. Values in bold indicate statistically significant effects. The reference levels for the categorical variables are *Flooded* (Flooding state) and *2015* (Year).

Avian biomass	**Variable**	χ^2	***p-value***
	Flooding state	16.900	***<0.001***
	Year	0.241	0.623
	Fortnightly survey	7.206	**0.007**
	Field size	38.407	***<0.001***
	Flooding state × Year	13.499	***<0.001***
	Flooding state × Fortnightly survey	15.895	***<0.001***

Figure S1. Photo collage illustrating the flooding state of rice fields when surveyed. Pictures A and B show dry fields (i.e., water layer height = 0 cm in more than 95 % of the field surface), whereas pictures C and D show flooded fields (i.e., water layer height > 0 cm in more than 95 % of the field surface). Photo credits: Albert Bertolero

Figure S2. Correlogram showing correlations (Spearman's correlations) among all local and landscape variables characterized. Positive correlations are displayed in blue and negative correlations in red. Size of circles and color intensity in the upper diagonal are proportional to the correlation coefficients (see the legend at the right side of the plot to associate colors and correlation coefficients in the lower diagonal). Only significant correlations are displayed (*P* < 0.01).

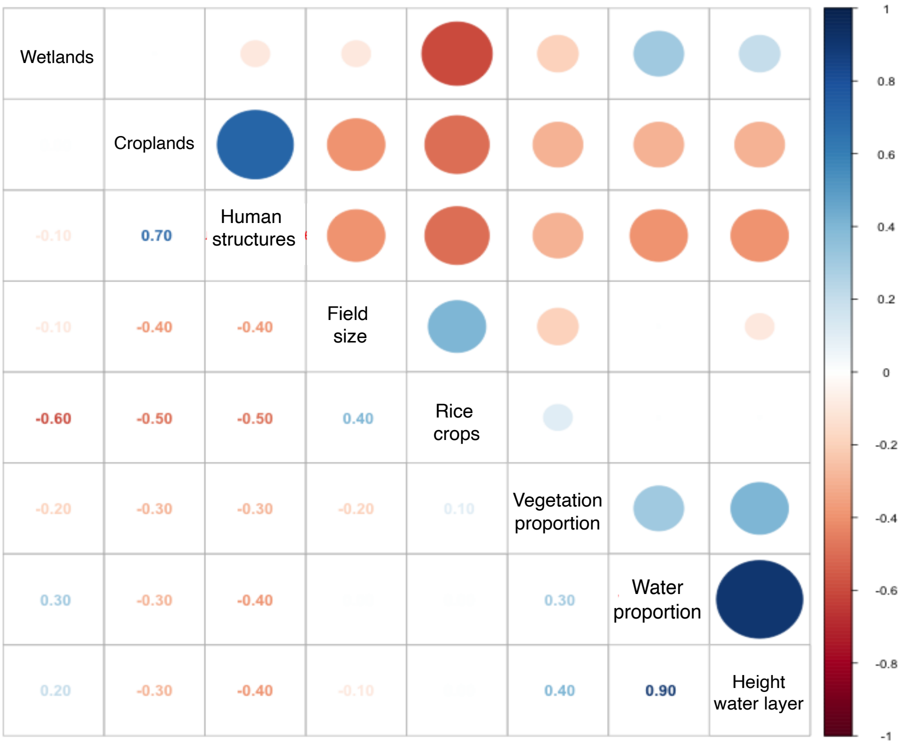

Figure S3. Interactive effect between fortnightly survey (fortnights since rice harvest) and flooding state on waterbird species richness (upper panel) and waterbird Hill Evenness (bottom panel). The figure is a direct output of the *visreg* R package.

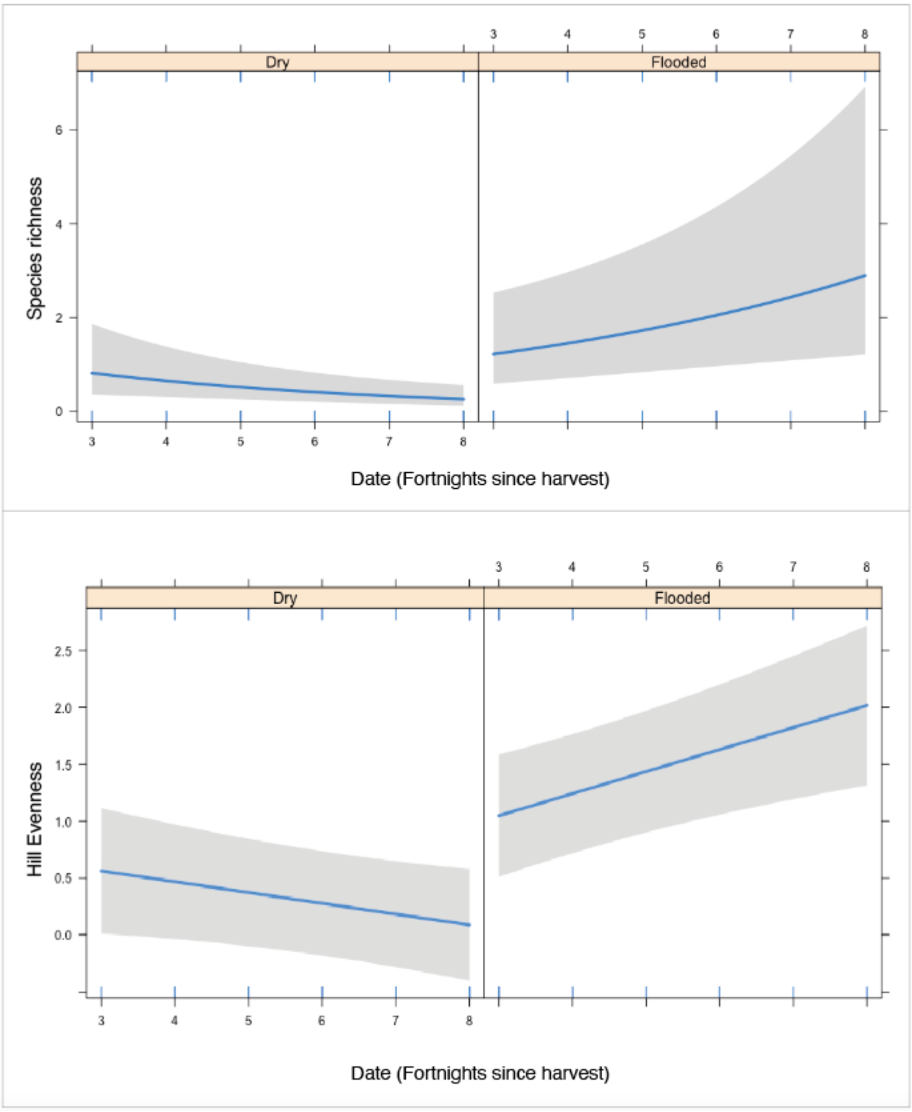

Figure S4. Avian biomass (Kg) in dry (2015: *n* = 57; 2016: *n*= 31) and flooded rice fields (2015: *n* = 33; 2016: *n*= 41) in the Ebro Delta. Small semi-transparent points indicate observed biomass for each field and fortnightly survey. Large solid points and error bars indicate the estimated means and the standard errors provided by the GLMMs, respectively.