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Ecological drivers of change in waterbird communities of Iranian wetlands

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ABSTRACT

With climate change, the increasing frequency of extreme weather and variability in climatic conditions have major impacts on wetland ecosystems, especially in arid regions such as south-west Asia. Iran hosts critical habitats and stopover sites for approximately 1.9 million waterbirds, yet its wetlands are threatened by extreme weather events, variation in climatic variables and human activities such as dams. We here assess how droughts and the variation of frost events in combination with increases in retained water behind dams impact waterbird communities in Iran. We used 10-year ranger-collected data (2013–2022) of 132 waterbirds in Iranian wetlands (n = 22), and applied Bayesian generalised linear mixed models to quantify effects of droughts (indicated by a negative standardised precipitation index SPI), rainfall, number of frost days, dam water surface (proxied by the water retained by the dam), vegetation cover, and wetland water surface on total abundance and richness of waterbird species. Our results show that waterbird richness increased in wetter periods but declined as dam water surfaces expanded. Specifically, a decrease of one-unit SPI was associated with an average decrease of three species per wetland and an increase of 25 km^2 in dam water surface was associated with an average decrease of three species downstream per wetland. Furthermore, an increase of 30 frost days corresponded to an average decline of 5548 ± 1910 individual birds per wetland (n = 220). These findings suggest that rising volumes of water behind dams in upstream wetlands is likely to exacerbate pressure on waterbirds from extreme weather events.

1. Introduction

Wetland ecosystems are increasingly threatened by human activities and climate change worldwide (Prakash and Verma, 2022; Shivanna, 2022), and particularly so in arid regions (Faramarzi et al., 2013; Khelifa et al., 2021). The wetlands of arid regions serve as critical habitats and stopovers for many waterbirds (Donnelly et al., 2020; Nagy et al., 2022). Evidence suggests that climate change can increase the variation in climatic variables and frequency of extreme weather events, which can have a greater impact on population abundance than the change of mere averages (Ummenhofer and Meehl, 2017; Cohen et al., 2020; Intergovernmental Panel on Climate Change (IPCC), 2023). Furthermore, the combined effects of human activities, extreme weather events and climatic variability are also substantial (Oliver and Morecroft, 2014; Maxwell et al., 2019; Newbold, 2018), as extreme weather events are becoming more intensive in regions with higher anthropogenic pressures (Ummenhofer and Meehl, 2017). Among the most prominent extreme weather extreme are droughts, which are defined as a prolonged periods of low rainfall resulting in a shortage of water (Dai, 2013). Droughts affect waterbird richness and abundance by altering the availability of their habitat (Albright et al., 2010; Gao et al., 2023).

An increase in variation in climatic variables such as frost days can also impact waterbird communities, mainly through increases in the likelihood of wetland water surface becoming frozen, thus making food less available for waterbirds (Selwood et al., 2018). Despite the detrimental effect of frost days on waterbird populations, there is only a single study that has shown that an increase in frost days may influence an earlier departure time for waterbirds (Wu et al., 2019), but there is no information on how the variation in frost days affects the richness and abundance of waterbirds over time. The impact of droughts on the richness and abundance of waterbirds seems to be complex. For instance, an increase in the frequency of droughts can lead to declines in

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vegetation cover, which in turn, reduce the availability of habitat and food resources for some waterbird guilds such as herbivorous waterfowl (Selwood et al., 2018; Goldstein et al., 2024). In addition, an increasing frequency of droughts could also be associated with human activities (Diffenbaugh et al., 2015). For instance, an increase in the water retained behind a dam affects both the species richness and abundance of waterbirds by decreasing the availability of water in wetlands further downstream (Wu et al., 2019). Although the impact of dams on wetlands downstream is well understood (Tamisier and Boudouresque 1994; Hamdi et al, 2008), there is limited evidence on how the droughts and variation of frost days in combination with increases in retained water behind a dam upstream affects waterbird richness and abundance in wetlands.

The effects of extreme weather events, such as droughts on habitat structure (e.g., vegetation, wetland water surface) and food resources is more pronounced in certain guilds (Cohen et al., 2020). Indeed, the sensitivity and response to droughts may vary among waterbirds with different ecological traits. While earlier studies have mostly focused on the impact of drought on bird richness and abundance (Mac Nally et al., 2009; Albright et al., 2010; Nimmo et al., 2016; Goldstein et al., 2024), these studies have overlooked guild-specific responses of waterbirds to drought (Albright et al., 2010; Özgencil et al., 2020). Furthermore, examining only droughts without including other extreme weather events is unlikely to provide sufficiently reliable and detailed information for understanding the effects of extreme weather events on different waterbird guilds (Carroll et al., 2017). This highlights the necessity of assessing the additive effects of droughts, variation in frost days, and increases in the retained water behind impacts on waterbird guilds to improve the management of wetland habitats that support all waterbird guilds (Gao et al., 2023).

Iran, located in southwest Asia, has 84 coastal and inland wetland sites, 25 of which are recognized as Ramsar sites (Daryadel and Talaei, 2014). Most of the wetlands in Iran are internationally recognized as important wintering grounds for both common and globally endangered birds, as many waterbirds migrate through the country as they navigate the African-Western, Siberian, Caucasus, and Eurasian flyways (Kirby et al., 2008). This underscores the importance of Iran's wetlands in providing wintering habitats for waterbirds in the Middle-East (Nourani et al., 2015). Iranian wetlands support approximately 1,900,000 water birds, accounting for 5 % of the global water bird population (International Waterbird Census (IWC), 2021). Despite the considerable contributions of Iranian wetlands in supporting waterbirds, in recent decades, these wetlands have faced many challenges. The most significant threats to Iran's wetlands are prolonged droughts (Sanjerehei and Rundel, 2017; Mirakbari and Ebrahimi-Khusfi, 2021) and extensive dam construction (Maghrebi et al., 2023). For example, between 1995 and 2010, the construction of 43 dams led to seven meters decrease in the depth of the Ormia wetland in southwestern Iran (Ouria and Sevinc 2016), which indicates how retaining water behind dams upstream impacts this wetland. Furthermore, a study by Rahimi and Hejabi (2018) showed that while there was a decreasing trend in the number of frost days in Iran, the variation in the number of frost days across many regions of Iran has increased, with a fluctuation of 30 days between 2008 and 2015 and the variation of frost days in Iran appears to be more pronounced at local scales. However, there is still no evidence on how variation in frost days and drought along with increases in water retained behind dams upstream affect the richness and abundance of waterbird populations in Iran.

In this study, we aimed to assess the impacts of extreme weather events, including the number of frost days and droughts along with dam construction as the most prominent human activities in the wetland upstream on waterbirds. We used a decadal dataset (2013–2022) collected by rangers and applied Bayesian generalized linear mixed model to test the following three hypotheses:

(1) The effects of drought can be exacerbated by increased water retention behind upstream dams, further reducing the richness and abundance of waterbirds (Gao et al., 2023; Martins et al., 2024).
(2) The variation in frost days would negatively affect both the richness and abundance of waterbirds in Iranian wetlands.
(3) Wetland water surface area, number of frost days, droughts, and vegetation cover are expected to affect both the richness and abundance of waterbirds, as well as richness and abundance at the guild level (e.g., ground-gleaners and reed-dwellers).

2. Methods

2.1. Study region

Our study area encompassed 22 wetlands in Iran, covering a total of 11,740 km^2, with 15 of these wetlands listed as Ramsar sites. According to Iran's climatic classification, our studied wetlands fall within the three macro-bioclimatic zones. The first zone is the Temperate zone to the south-west of the Caspian Sea such as Anzali, Boujagh and Amirkalaieh, the second is the Mediterranean zone, characterised by mild winters and dry summers. The Mediterranean climate includes the majority of our studied wetlands. For example, Miankaleh and Ghomishan located to the south-east of the Caspian Sea, are part of the Mediterranean pluviseasonal-oceanic bio-climate (Djamali et al., 2011). The Mediterranean xeric oceanic region includes Mighan, Ajigol-Alagol, Almagol, Arzahn and Maharlou, and northern Urumia. However, wetlands alongside the Zagros mountains such as Zarivar, Choghakhor and Gandoman as well as southern Urumia lake and its surrounding wetland are included within the Mediterranean pluviseasonal–continental bio-climate. Horlazim and Gavkhoni are encompassed by the Mediterranean desertic–continental bio-climate and the third zone is dominated by a tropical desert bio-climate (Djamali et al., 2011). That zone includes the Tropical Wetlands Shadegan and Khlij Govater (See Fig. 1).

2.2. Ranger-collected bird data

We use extensive waterbird census data (2013–2022) systematically collected by Iranian rangers across wetlands during non-breeding season. Since 1976, the Iranian Department of Environment (DoE) conduct the annual waterbirds census following the waterbird census scheme protocol provided by the International Waterbird Census (IWC) (Amini, 2006). Rangers in Iran are responsible for monitoring wildlife including waterbirds and mammals (Soofi et al., 2022b). The censuses of waterbirds follow a standard protocol with fixed observation points, which is consistently implemented during January each year (Amini, 2006). These fixed observation points are located along the shoreline and across different wetland habitat types to ensure comprehensive coverage. The number of observation points varies by site depending on wetland size, typically ranging from 3 to over 10 per site. The census teams consist of a skilled environmental expert specialised in waterbird surveys, being accompanied by rangers (Amini, 2006). To minimize the counting errors and enable annual comparisons, the same individual rangers (where possible) conduct the annual censuses at each site (Buckland et al., 2015). To avoid double-counting, in particular at neighbouring wetland sites, waterbird counts are conducted consecutively without interruption (Amini, 2006). If a counting point became flooded due to changes in the water level in a given year, a boat was used to access the site (Amini, 2006).

Furthermore, wetland sites are typically divided into multiple sighting points, where rangers count the number of birds for each species. The total number of waterbirds across the entire site is calculated by aggregating the counts of each species observed at sighting localities. For most wetland sites, sighting points are located along the shoreline and are distributed across various wetland habitat types (Delany, 2010). Typically, the maximum distance that birds were recorded is 500 m.

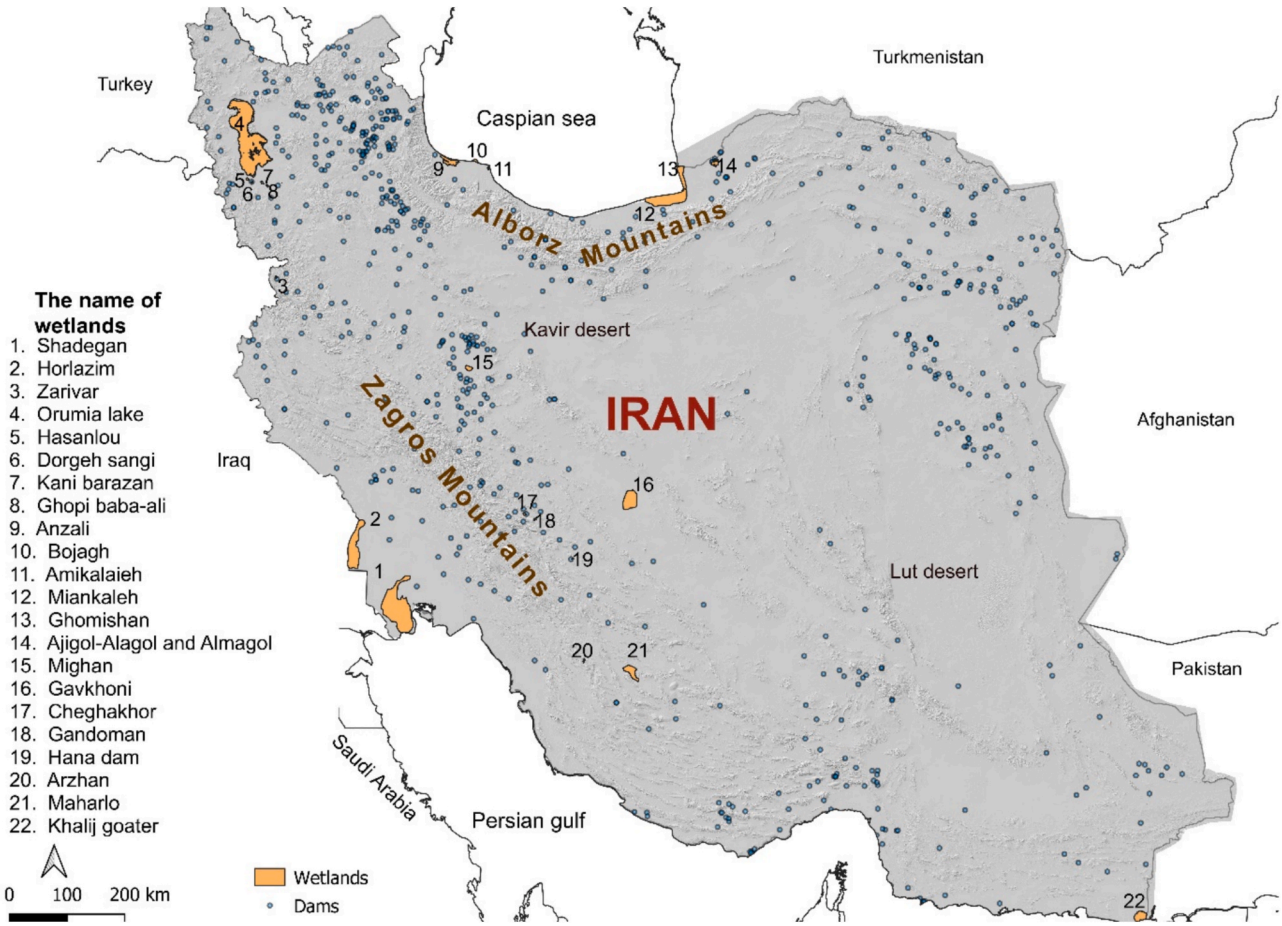

Fig. 1. Distribution of dams (blue circles) and studied wetlands (orange polygons) across Iran. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Observers use binoculars (typically 8 × 42 or 10 × 50) and spotting scopes (20–60 × zoom) to identify and count birds. The counting method follows a total count approach, where all visible individuals of each species are recorded from each point. Birds were identified by sight within a 360° field of view. To maintain consistency in bird monitoring across years, rangers do count birds in the same manner each year at fixed locations (Malekian et al., 2022). However, The bird counts take place in clear, sunny weather conditions from 6:00 am to 6:00 pm, with the same observers (i.e., rangers) conducting the count each year to reduce observer bias (Buckland et al., 2015).

2.3. Determining functional groups

To determine the functional groups of the waterbirds, we created a database comprising 10 bird traits, primarily related to diet, foraging habits, and body mass (Laliberté and Legendre, 2010). Information on these bird traits was gathered from various resources, as well as from the international bird trait databases (Wilman et al., 2014; Tobias et al., 2022). Subsequently, we built a distance matrix by using Gower distances (Podani, 1999), which enables the inclusion of categorical and numerical traits. The calculation of Gower distance was carried out by using the 'FD' R package (Grenié and Gruson, 2023). We used a distance matrix to generate a dendrogram tree, and visually segmented the tree into five primary functional groups: ground gleaners, reed-dwellers, omnivorous birds, wading birds and fish-invertebrate feeders. (see the Supplementary file, Fig. S8, Tables S1 and S2).

2.4. Climate data

Monthly climatic data were obtained from the Iranian Meteorological Organization (https://www.irimo.ir) from 2013 to 2022. We placed a 20 km buffer around each wetland site, and meteorological data from this buffer were used to assess the impact of extreme weather events on bird richness and abundance (McIntyre et al., 2019). We also considered climatic conditions in the month leading up to survey period (January), as they can influence bird richness and abundance during the surveys (Askeyev et al., 2018). Consequently, we calculated the climatic variables late October when migratory birds arrive until end of January when waterbird survey was conducted (Table 1). For each year, we measured rainfall, and the minimum temperature during these four months (October to late January). Additionally, we counted the number of days with temperatures below zero within each site from October to late January in each year (Moberg and Jones, 2004). We considered the standardized precipitation index (SPI) as a proxy for drought conditions across wetland sites in Iran (Odongo et al., 2023). We calculated the climatic variables as:

$$SPI = (p\text{-}p^*)/\sigma p$$

where p indicates the rainfall during a certain time period and p* denotes the mean rainfall for the same time period and σ_p is the standard deviation of rainfall for a long-term rainfall value for the same period (Aryal et al., 2009). SPI ranges from −3 to + 3, and negative values indicate dry periods, whereas positive values represent wet periods. Detailed information on climatic variables are provided for each studied wetland in the Supplementary file (Figs. S3 and S4).

Table 1
Predictor variables used in the models, their unit, description, hypothesis and source.

Variables	Unit	Description	Hypothesis	Source
Rainfall	Millimeters (mm)	The rainfall variable is the total amount of rainfall (rain, snow, sleet) accumulated over a specific 6 month period (from October to late January), typically expressed in millimeters (mm)	We hypothesized that the rainfall would positively affect the richness and abundance of waterbirds by increasing water surface and help vegetation growth	(Reid et al., 2022)
Standardized precipitation index (SPI)	the unit of the SPI is the standard deviations.	The Standardized precipitation index (SPI) is a widely used index in climatology and hydrology to quantify the deviation of observed rainfall from its long-term average, The SPI helps in detecting droughts and excessive wet periods by transforming raw rainfall data into a standardized score. SPI values typically range between −3 and + 3. The positive value represents a wet period, while the negative value a dry period.	We expected that a decline in SPI would result in a decline in the richness and abundance of waterbirds.	(Malekian et al., 2022)
Number of frost days	Days	The frost day index is defined as the number of days in a year with a daily minimum temperature below 0 °C	We hypothesized that an increase in the number of frost days would significantly impact the richness and abundance of waterbirds, primarily by restricting food availability through the freezing of water bodies and vegetation.	(Xu & Si, 2019)
Vegetation cover	Square kilometer (km^2)	Vegetation cover refers to the proportion of soil or ground covered by green plants and in this study, it is quantified by Enhanced Vegetation Index (EVI).	We expected that the richness and abundance of some waterbird guilds such as herbivorous and reed-dwellers would be positively influenced by vegetation cover, because it can provide food and shelter for waterbirds, in particular herbivorous birds and reed-dwellers.	(Selwood et al., 2018)
Wetland water surface	Square kilometer (km^2)	A wetland water surface is an area of a wetland that remains covered by water, providing critical habitat and resources for aquatic and semi-aquatic species	We expected that reductions in the wetland water surface area would reflect the negative impacts of extreme weather events and dam construction, leading to decreases in the richness and abundance of waterbirds, especially those that are highly dependent on water surfaces	(Faramarzi et al., 2013; Gyurácz et al., 2011)
Dam water surface	Square kilometer (km^2)	Dam water surface refers to the area of water that accumulates behind a dam, forming a reservoir or lake	We hypothesized that an increase in the water surface area behind a dam could negatively impact the richness and abundance of waterbirds by disrupting natural water flows to wetlands and increasing the likelihood of wetland drying	(Martins et al., 2024; Wu et al., 2019)

2.5. Remotely sensed data

We used the Enhanced Vegetation Index (EVI) for the period from October to late January, to align with waterbird occurrence. EVI values range from −1 to + 1, where negative values correspond to non-vegetation surface, and positive ones indicate vegetated areas (Gurung et al., 2009). We used Landsat 8 (OLI) images from 2013 to 2022 and processed them by filtering out covering pixels using the BQA bit 4, as well as pixels with low cloud shadow confidence (Gross et al., 2022). After filtering, we calculated the mean EVI from October to late January for each year and set a threshold of 0.2 to identify vegetated areas (Verhegghen et al., 2014). We then calculated the total area of the wetlands with mean EVI values above this threshold as a proxy for vegetation cover (Kong et al., 2019). We used the Google Earth Engine to conduct all these analyses. Finally, to map wetland and dam water surface, we used data from the Global Surface Water Explorer (https://global-surface-water.appspot.com/). We calculated the mean water surface area for each wetland from October to late January (2013–2022). Lastly, we calculated the mean water surface area behind all dams within each wetland watershed for the period from October to late January. (see the Supplementary file, Figs. S5 and S6).

2.6. Statistical analyses

To test our hypotheses, we employed a Bayesian generalized linear mixed model using the 'brms' (Bayesian multi-level regression model) R package (Bürkner, 2017) in Stan with the interface R version 4.2.3 (R Core Team, 2023). This modelling approach assumes the latent variable (i.e., equivalently the error term ε) to be normally distributed (Bürkner, 2017). We fitted three separate models on: (1) bird abundance (i.e., sum of the counts for all species), (2) bird richness (i.e., sum of the numbers for all species) and (3) specific bird guilds. We standardised (mean = 0, standard deviation SD = 1) all the hypothesised predictor variables (Table 1). We avoided to include a covariate if its coefficient was equal or greater than to the cut-off point of $|rho| \geq 0.7$ (Dormann et al., 2013) (Fig. S7).

2.6.1. Modelling

We began our modelling process by including each variable individually to identify a variable −specific effect on the response variables (i.e., bird abundance, richness). Next, we ranked all these single-variable models using the one-leave-out cross validation method (LOO-CV). This step enabled to identify the covariates with a substantial effect on the response variable. After selecting the influential covariates from the top models, we subsequently expanded our models by adding covariates in the single-variable models (Kéry and Royle 2016; Soofi et al., 2022b). We fitted our models with three distribution functions including Poisson, negative-binomial (NB) and zero-inflated Poisson. Finally, our models have favoured the negative-binomial distribution over the other two distributions, which accommodates the over-dispersion parameter (Kéry and Schaub 2011; Vehtari et al., 2021). We assumed that bird richness and abundance (C_{it}) would vary simultaneously at site i (hereafter referred to as wetland-site) and year t (i.e., scaled variable) levels (Kéry and Schaub 2011; Kéry and Royle 2021). Variations in bird abundance or richness at wetland-site-year-specific levels may be influenced by local weather conditions, potentially forcing birds to move among wetlands. This movement could potentially introduce bias into the count outcomes (Schummer et al., 2010). To account for such biases, we therefore included wetland-site as a random intercept (alpha, α_0) and site-specific regression (1 | site) with year trend variable (0 + wetland-site || year-trend). This allows the wetland-site to vary by year-trend, but forces the slope (i.e., beta, β) for each wetland site to be uncorrelated across different levels of year-trend (Kéry and Royle 2021).

The Bayesian 'glmm' for richness and abundance model was defined

as follows:

$C_{i,t} \sim Negative\ Binomial\ (\mu_{i,t}, \theta)$.

where $C_{i,t}$ is the observed (or partially observed) bird count {0, 1, 2, 3, …} at each wetland-site i during year t (n = 22). $\mu_{i,t}$ represents the expected mean bird abundance, $\theta > 0$ is the dispersion parameter that determines the deviation from a Poisson distribution (Kéry and Schaub 2011). The NB distribution was chosen (variance exceeds the mean) to account for overdispersion in bird count and richness data (Hilbe 2011; (Kéry and Schaub 2011). Out model can be described as following:

where mu $\mu_{i,t}$ is the expected abundance or richness of the birds at year t.

$$log(number\ of\ rangers^{*}\mu_{i,t}) = \alpha_0 + \beta_1{}^{*}X_{SPI,i,t} + \beta_3{}^{*}X_{frost-days,i,t} + \beta_4{}^{*}X_{dam-water\ surface,i,t} + year_{i,t} + wetland_{,i} + \gamma i, t$$

wetland-site$_i \sim$ Normal (0, $\sigma^2_{wetland\text{-}site}$)

$year_{i,t} \sim$ Normal (0, $\sigma^2_{year,\ wetland\text{-}site}$)

where α_0 is the intercept, β denotes the fixed effect for the hypothesized variables and gamma γ denotes the shape of the dispersion parameter. The *wetland-site*$_{,i}$ is the random effect for grouping variable i (i.e., wetland sites) with mean 0 and the $\sigma^2_{wetland}$-site is the variance of the intercepts for each wetland site. σ^2_{year} indicates the variance of the slopes for each wetland site across different years (2013–2022), which assumed to be a normal random effect with mean 0. We used a weakly informative normal prior for all coefficients (mean $\mu = 0$, and a vectorized standard deviation $\sigma^2 = 10$) (Bürkner, 2017). We selected a student_t prior for random effect parameters (i.e., intercept wetland, wetland, year; $\mu = 3$, degree-of-freedom $\nu = 0$, $\sigma^2 = 2.5$) (Gelman et al., 2008; Bürkner, 2017). To obtain random samples from the posterior distribution, we used 6000 iterations with a 3000 iterations warmup across three parallel chains using the Markov Chain Monte Carlo (MCMC) algorithm. Model ranking was based on the leave-one-out cross validation (LOO-CV) technique (Vehtari et al., 2017). Our inferences were drawn from the results of the best-fitting model within each model set (Bürkner and Vuorre, 2019). We considered coefficients to have a substantial effect (i.e., significant) if their credible intervals (CrI) did not include 0, while coefficients with CrIs that marginally included 0 were regarded as having a less substantial effect (Benjamin et al., 2018). The number of rangers across wetland-sites was included as an additive offset, on a log scale (Kéry and Royle, 2021). We took this approach because our model does not directly accommodate the detection probability parameter. Instead, we aimed to minimize potential biases, which may arise from an unequal number of observers (i.e., rangers) conducting bird counts at each wetland site. Finally, we assessed the goodness of fit of our models using posterior predictive checks and visually checked the MCMC plots (Bürkner and Vuorre, 2019; Gimenez et al., 2024) (see Supporting Information).

3. Results

3.1. Overall richness and abundance

Overall, from 2013 to 2022, a total of 132 waterbird species were recorded across the 22 studied wetlands. The waterbirds numbers fluctuated between 670,000 individuals in 2019 and 431,000 individuals in 2020, with no visible trend. (Fig. 2). The largest waterbird numbers were counted in the Miankaleh wetland ecosystem, fluctuating between 31,372 and 216,573 individuals, and from 32 to 42 wetland bird species. The wetland with lowest numbers of birds was Ghopi baba-ali, ranging from 0 to 442 individuals (up to 5 species). The statistics for each wetland are found in the Supplementary file (Figs. S1 and S2).

According to our generalized linear mixed modelling results, the overall richness of waterbirds was positively associated with an increasing standardised precipitation index SPI ($\beta = 0.11$, 95 % CrI = 0.06 to 0.16), but decreased with increasing dam water surface ($\beta = -0.14$, 95 % CrI = − 0.26 to − 0.03) (Figs. 3 and 4). A decrease of one unit in the SPI can be expected to result in an average decrease of three species per wetland. As for dam construction, an increase of 25 km^2 in

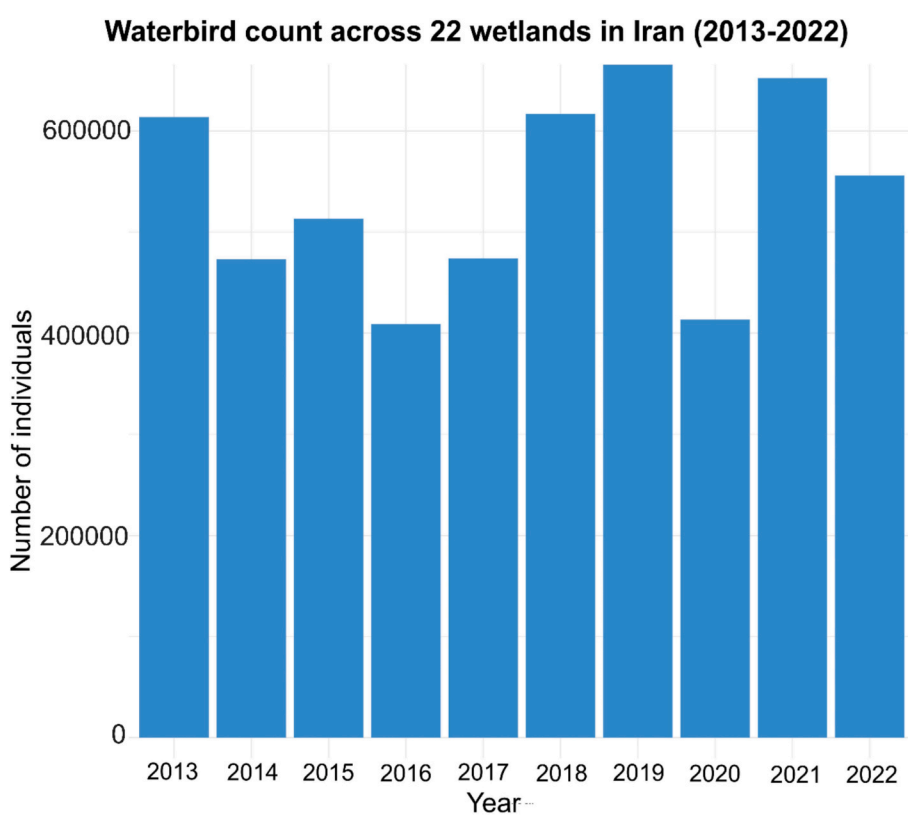

Fig. 2. Waterbird count across 22 wetlands in Iran (2013–2022).

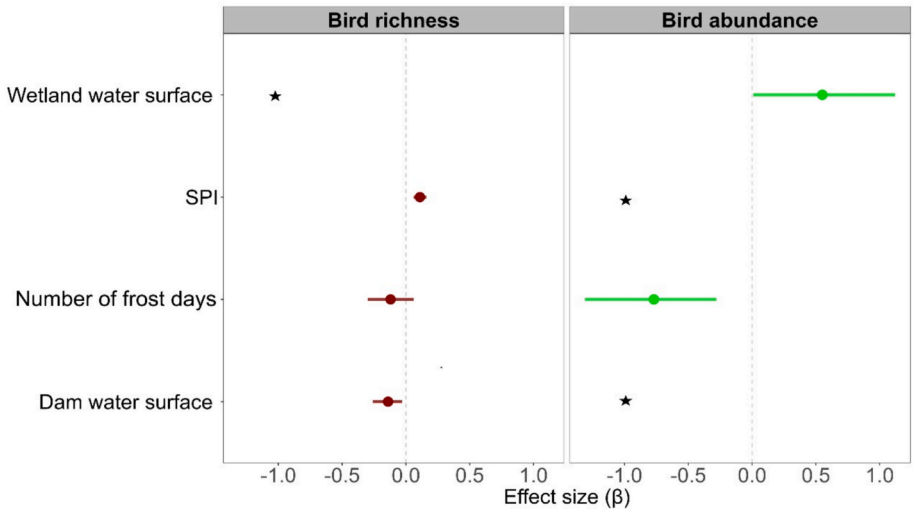

Fig. 3. Posterior means (beta coefficients) and their 95 % credible intervals (CrI) of the covariates of the best-fitting model estimated for the global model (including all species) of richness and abundance of waterbirds across 22 wetlands in Iran, based on ranger-collected data from 2013 to 2022. Variables not included in the best-fitting model are shown by asterisk sign (*).

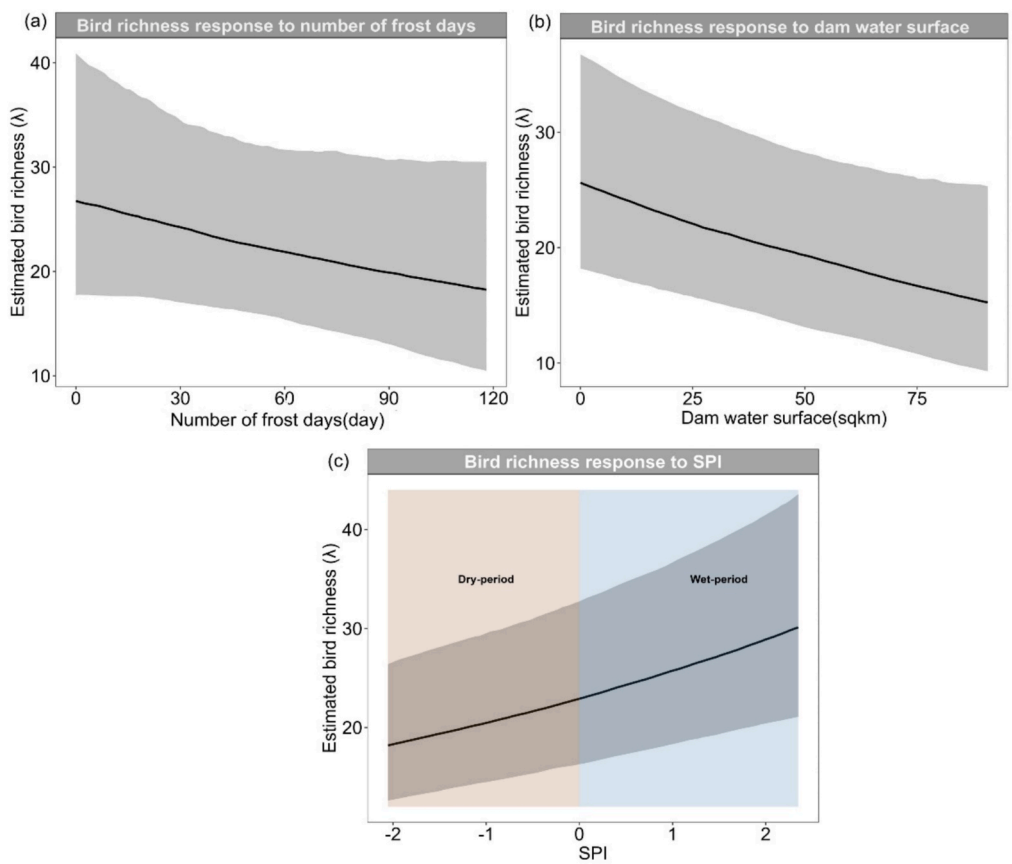

Fig. 4. Response curves of the estimated posterior mean (beta coefficients) of overall richness of water bids in relation to (a) number of frost days (b) dam water surface and (c) Standardized precipitation Index (SPI). The solid lines indicate the posterior means, while the shaded grey areas indicate the 95% credible interval bands.

water surface area behind the dams results into an average decrease of three bird species per wetland downstream (Fig. 4). Results further revealed that the number of frost days had a less substantial negative impact on waterbird richness ($\beta = -0.12$, 95 % CrI = − 0.30–0.06) (Fig. 3). Results of our abundance model revealed a positive influence of wetland water surface on the abundance of waterbirds ($\beta = 0.55$, 95 % CrI = 0.01–1.12). In contrast, the number of frost days had a substantial negative effect on the abundance of waterbirds ($\beta = -0.77$, 95 % CrI = − 1.31 to − 0.28) (Fig. 3). More specifically, an increase of 30 frost days likely results into an average decrease of 5548 birds per wetland (Fig. 5).

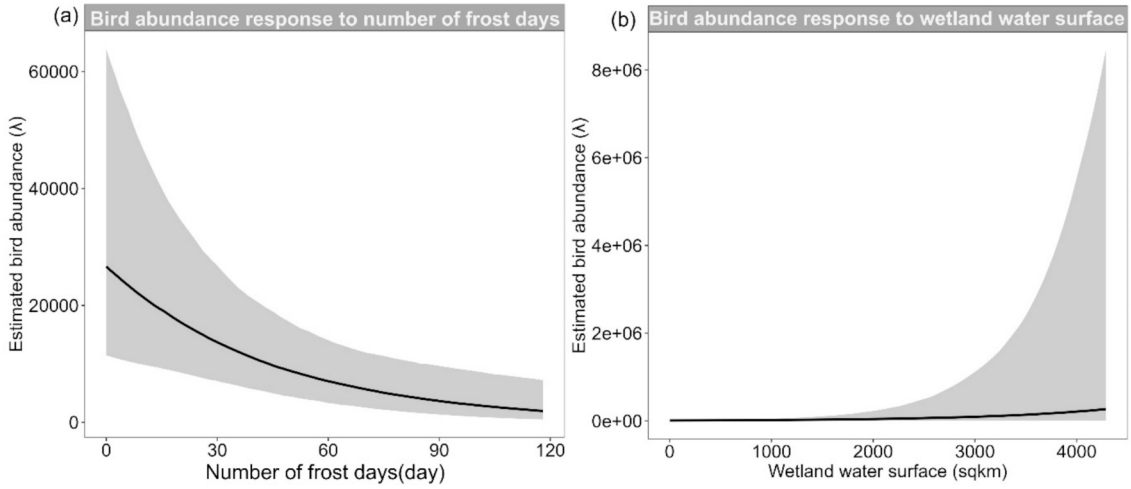

Fig. 5. Response curves of the estimated posterior mean (beta coefficients) of overall abundance of water bids in relation to (a) number of frost days (b) wetland water surface The solid lines indicates the posterior means and the shaded grey areas represent the 95% credible interval bands.

3.2. Guild-specific richness response

While dam water surface and SPI had a significant impact on overall species richness, they did not show significant effects on the species richness within waterbird guilds (Figs. 2 and 6). Our guild-specific richness models indicated that the richness of reed-dwellers was positively related to vegetation cover ($\beta = 0.20$, 95 % CrI = 0.05–0.35). Also, an increase in the wetland water surface area substantially increased the richness of ground-gleaners ($\beta = 0.17$, 95 % CrI = 0.06–0.28). In contrast, the richness of ground-gleaners decreased with increased rainfall (β = -0.26, 95 % CrI = − 0.37 to −0.14). Conversely, rainfall positively influenced the richness of reed-dwellers ($\beta = 0.29$, 95 % CrI = 0.14–0.43), omnivorous birds ($\beta = 0.17$, 95 % CrI = 0.07–0.27), and fish-invertebrate feeders ($\beta = 0.12$, 95 % CrI = 0.02–0.23) (Fig. 6). Furthermore, the number of frost days was strongly and negatively associated with the richness of wading-birds (β = -0.40, 95 % CrI = − 0.52 to − 0.29) as well as with the richness of fish-invertebrate feeders (β = -0.37, 95 % CrI = − 0.47 to − 0.26) (Fig. 6; Supplementary file, Fig. S10).

3.3. Guild-specific abundance response

We found that the SPI had a positive and substantial effect on the abundance of the majority of waterbirds, including reed-dwellers (β = 0.80, 95 % CrI = 0.51–1.27), ground gleaners ($\beta = 0.36$, 95 % CrI = 0.11–0.62), fish-invertebrate feeders (β = 0.28, 95 % CrI = 0.06–0.51), and omnivorous birds (β = 0.24, 95 % CrI = 0.04–0.44) (Fig. 7). Similarly, rainfall had a substantial and positive effect (β = 0.67, 95 % CrI = 0.31–1.04) on the abundance of wading birds (Fig. S9). Wetland water surface area had a substantial and positive effect on the abundance of ground gleaners (β = 1.16, 95 % CrI = 0.19–2.13) and fish-invertebrate feeders (β = 0.8, 95 % CrI = 0.2–1.54), whereas the influence of wetland water surface on reed-dwellers was less substantial (β = −0.5, 95 % CrI = −1.55–0.52) (Fig. 7). The overall abundance of waterbirds declined with an increasing number of frost days, but no such effect was observed in the abundance of individual guilds (Figs. 2 and 7).

Furthermore, ground gleaner abundance was less substantially associated with vegetation cover ($\beta = 0.68$, 95 % CrI = 0.27–1.69). The guild-specific abundance models also showed that the abundance of fish-invertebrate feeders was negatively and substantially impacted by increasing dam water surface area ($\beta = -1.46$, 95 % CrI = −2.05 to

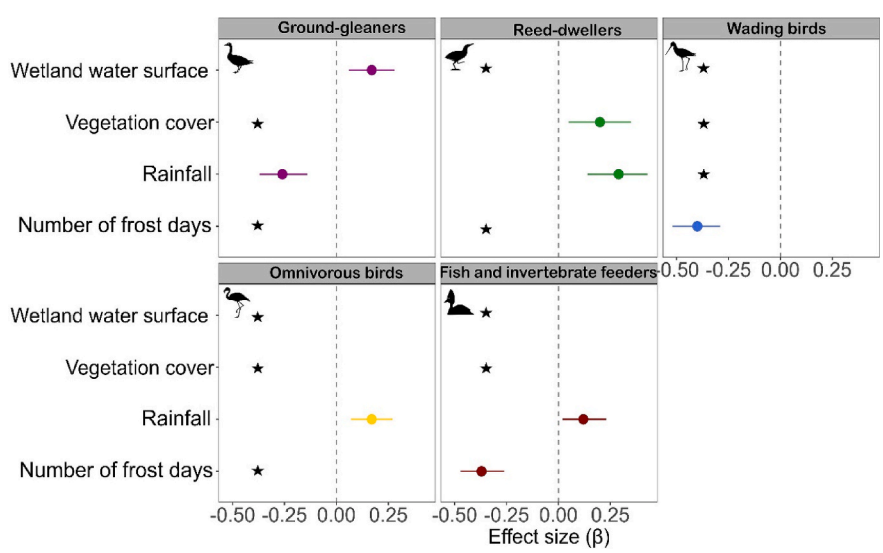

Fig. 6. Posterior means (beta coefficients) and 95% credible intervals (CrI) of covariates of the best-fitting model estimated for the richness of water bird guilds. The asterisk symbol indicates that the variables were not part of best-fitting model.

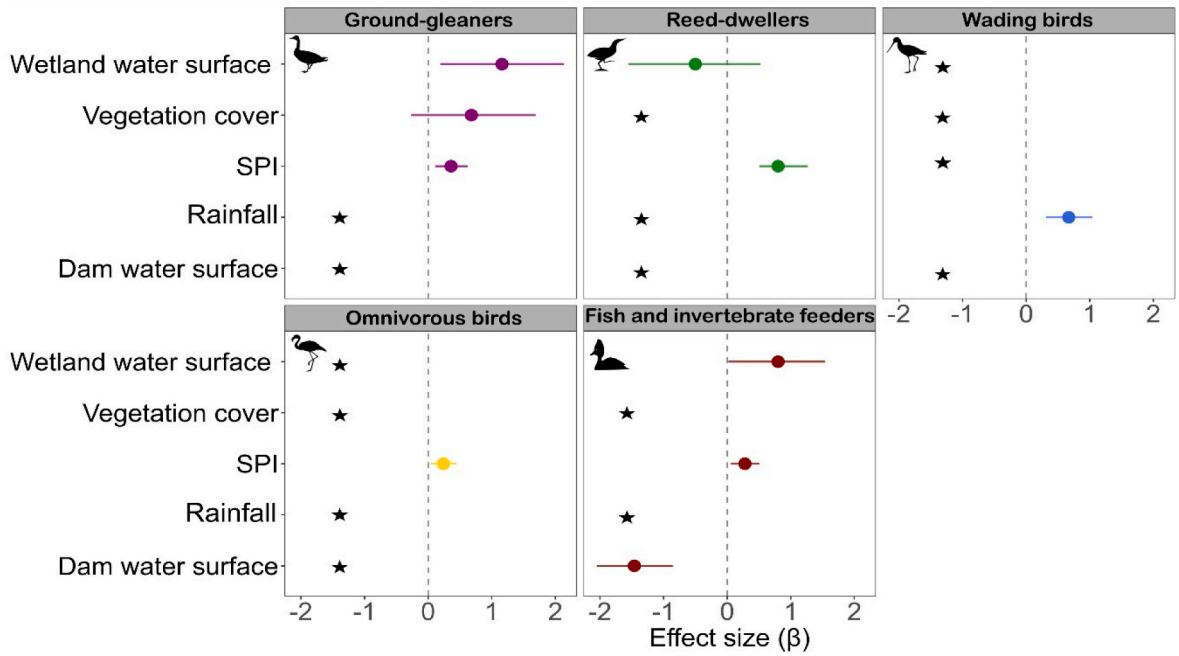

Fig. 7. Posterior means (beta coefficients) and 95 % credible intervals (CrI) of the covariates of the best-fitting model estimated for the abundance of water bird guilds. The asterisk symbol indicates that the variables were not part of best-fitting model.

−0.85). The goodness of fit test for our best-fitting models showed a reasonable fit, with the simulated data (posterior predictions) following the observed data. In addition, the Gelman-Rubin statistic (Rhat) values were 1.00 indicating that models were well converged (Tables S3–S5; Figs. S11–S25).

4. Discussion

Our findings contribute to the growing evidence that wetland ecosystems in arid regions, along with their waterbird communities, are increasingly vulnerable to the combined impacts of climate change human-activities (Erwin, 2009; Prakash and Verma, 2022; Shivanna, 2022). In particular, we show that variation in frost days, drought intensity, and water retention behind dams significantly affect waterbird richness and abundance, underlining global concerns about the susceptibility of wetlands to both climate change and anthropogenic pressures (Ummenhofer and Meehl, 2017; Cohen et al., 2020).

4.1. Overall richness and abundance

The finding supports our first hypothesis regarding the negative effects of droughts and increases in water retained behind dams on the overall richness of waterbirds. However, the effects of droughts and increases in water retained behind dams on overall bird abundance were not substantial. We found that a decline in the SPI value may on average lead to a decrease of approximately three waterbird species per wetland, highlighting the negative impact of droughts on the richness of waterbirds. This finding is in line with previous studies, which reported that droughts contribute to declines in the richness of waterbirds by reducing the moisture of the soil, hindering plant growth and decreasing water availability (Thompson et al., 2009; Albright et al., 2010; Carroll et al., 2017; Gao et al., 2023). Our results also revealed that this condition can be further exacerbated by increases in water retained behind dams further upstream. We estimated that an increase of 25 km^2 in water storage behind dams would lead to a decline of three species per downstream wetland. In practice, the construction of upstream dams could result in water recession and prevents water from flowing into wetlands downstream (Wu et al., 2019; Abreu et al., 2020). Iran is among the top countries in the world when it comes to dam constructions (ranking third), with 647 dams currently in operation and 146 under construction (Maghrebi et al., 2023). Such large-scale dam construction across the country poses a significant threat to wetlands and their associated bird populations. This is particularly concerning in semi-arid and arid region wetlands, where water shortage caused by extreme weather events like prolonged droughts pose a serious threat (Khelifa et al., 2022). For example, several wetlands in Iran, such as Ormia Lake in the north-west, as well as Gavkhoni and Mighan which serve as crucial wintering stopover for many migratory birds are now partially dry (Rahimi et al., 2023), largely due to the excessive construction of dams and prolonged drought (Sanjerehei and Rundel, 2017). This underscores the need for sustainable water resource management that allows for adequate water flow into wetlands. However, these natural flows have been prevented by reduced river discharge that feeds the wetlands. Maghrebi et al (2023) further reported that river discharge in Iran has experienced a decreasing trend, being 2.5 times greater than the global average. More concerningly, this rate is much higher in central Iran, where the climate is classified as arid and the likelihood of drought is higher (Madani et al., 2014; Rahimi et al., 2023). This situation may lead to continued reductions in wetland water levels (Rahimi et al., 2023) and further declines in waterbirds. Our findings also demonstrate a considerable influence of wetland water surface area on the abundance of waterbirds, but not on their richness. This can be attributed to the direct and immediate impact of increased wetland water surface on the abundance of waterbirds due to the expansion of available habitat (Gyurácz et al., 2011; Hohman et al., 2021). The results also supported our second hypothesis, indicating that an increase of 30 frost days on average can result in a decline of 5548 birds per wetland. This decline highlights the broader ecological consequences of wetland degradation associated with prolonged frost periods in Iran. Increases in variation in frost days can lead to frozen ground conditions, potentially making habitat inaccessible for waterbirds (Estiarte and Peñuelas, 2015) and driving birds to seek for alternative foraging areas (Fayet et al., 2021).

4.2. Guild-specific richness and abundance

For our waterbird functional trait analysis, we used data from international bird trait databases (Wilman et al., 2014; Tobias et al., 2022), which closely match the characteristics of waterbirds observed in Iran. Our guild-specific results showed that the wading-bird (e.g. plovers, stints, and sandpipers) and fish-invertebrate feeders (e.g. pelicans, grebes, and mergansers) were among those appearing to be highly vulnerable to variation in frost days. Presumably, the foraging habitat of this guild depends heavily on the water surface availability and increase in the number of frost days may limit the ability to forage and access critical resources (Aharon-Rotman et al., 2017). While frost days significantly affected the species richness of wading birds and fish–invertebrate feeders, they had no detectable impact on their overall abundance, suggesting that frost may disproportionately affect less numerous or more specialized species within these guilds.

In addition, we show that the sole increase in wetland water surface area does not necessarily result in a rise in the richness of all waterbird guilds, while other factors such as habitat heterogeneity also play an important role (Cerda-Peña and Rau, 2023). Our guild-specific richness models indicated that rainfall substantially affected the richness of most guilds. The richness of ground-gleaners (e.g. geese, cranes, and shelduck) was negatively affected by rainfall, but positively correlated with wetland water surface area. This suggests that, although increased rainfall may reduce grassland coverage, the expansion of wetland water surfaces can simultaneously create favourable conditions for ground-gleaners, presumably by enhancing access to shallow water zones and adjacent wet grasslands (Timmermans et al., 2008; Aharon-Rotman et al., 2017).Our model for reed-dwellers (e.g. Eurasian Bittern and Water Rail) showed that the richness of this guild is positively influenced by both rainfall and vegetation cover. This implies the necessity of preserving vegetation around wetlands to meet this guild's habitat requirement. The abundance of all ground-gleaners, reed-dwellers, omnivorous birds and fish-invertebrate feeders showed a positive trend with decreasing droughts, as a reduction in droughts benefits these guilds in various ways. For instance, increasing wet periods may positively influence the abundance of the fish-invertebrate feeder guild by creating potential habitats for algae, invertebrates and fish, which serve as the primary food resources for members of this bird guild such as grebes and mergansers (Mitsch and Gosselink, 2015). However, although extended wet periods may be favourable for some bird guilds they can be detrimental to others with different ecological requirements (Tavares et al., 2015). For example, we found that the abundance of reed-dwellers increased substantially during wet periods, but it was negatively affected by the expansion of water surface area. Indeed, reed-dwellers, such as bitterns, mostly prefer habitats dominated by reed (e.g., *Phragmites australis*) plants, which provides both shelter and feeding areas (Flis et al., 2024). The maintenance of these habitat depends on a delicate water balance, as both excessive and insufficient water can negatively affect them (Timmermans et al., 2008). Overexpansion of wetland water surface area may disrupt this balance by exceeding the waterlogged levels favoured by these birds, thereby reducing their abundance (Flis et al., 2024). Our results further showed that the abundance of ground-gleaners increased with increasing the expansion of wetland water surface, and to a lesser extent, with vegetation cover. This finding is in line with previous studies, which highlighted that wetlands characterized by a mosaic of open water and vegetative patches are vital for the persistence of ground-gleaners. These birds depend on both terrestrial habitats and aquatic environments for foraging and resting (Naugle et al., 1997). In a similar context, Wang et al. (2021) showed that ground gleaners like geese and cranes typically tend to feed on plants at early growth stages, which are negatively impacted by prolonged dry periods. Our results on reed-dweller and ground-gleaner abundance highlight the importance of maintaining both wetland water bodies and vegetation cover to support the persistence of all bird guilds, including reed-dwellers as well as ground gleaners. These findings indicate that conservation efforts should prioritize a heterogeneous mosaic of water and vegetation cover within wetland systems, rather than focusing solely on expanding water surface area (Ma et al., 2010; Tavares et al., 2015). Our results further showed that fish–invertebrate feeders appeared to be the only guild likely susceptible to increases in water retained behind dam. This vulnerability may be related to the dependence of these birds (e.g. grebes) on specific water levels that support their diving foraging habits (Paracuellos, 2006).

Our findings emphasized a discrepancy in how extreme weather events and retained water behind dams influence waterbird communities at different ecological scales. For example, while dam water surface and SPI significantly affected overall species richness, they did not show a significant impact on species richness within waterbird guilds. This suggests that, although the overall waterbird community was affected by drought and dam water surface through changing hydrological conditions, the richness of functional guilds remained stable, presumably due to niche saturation (Eisenhauer et al., 2023). Also, we observed that the overall waterbird abundance declined with an increasing number of frost days; however, this effect was not reflected within specific guilds, signifying that species within each guild may respond differently to frost, resulting in compensatory dynamics that mask guild-level changes (Rosenfeld, 2002). Collectively, these results underscore the importance of incorporating both community level and guild-specific responses to better understand the impact of environmental stressors on waterbird communities (Arruda Almeida et al., 2018).

Overall, with this study we gained further insights into the impacts of extreme weather events and climatic variability and how the increases in retained water behind dam affect the abundance and richness of wetlands birds in Iran. Nevertheless, a few drawbacks remain: First, we used the area of water surface behind dams as an indicator of dam impacts on the wetlands downstream. Ideally, we would recommend using water level and water depth which could be more precise indicators for determining the specific impacts of dams on water variation in the wetlands, but such data were not available for the wetlands we studied. Second, we acknowledge that the presence of waterbirds in wetlands can be governed by weather conditions at much larger scales. For example, in some years when wetland habitats in Iran are less habitable for waterbirds, they might migrate and move further north to wetlands in Turkmenistan or further south to other Persian Gulf countries, which could result into potential spillover effects in the bird population that we studied. However, we didn't have data from these regions to include in our analysis. Nevertheless, we mitigated the potential spillover effect in our negative binomial models by incorporating random effects (i.e., wetland-site, year), which account for the latent spatial variability across wetland sites and temporal variability over time. Additionally, our model did not accommodate for detection probability, because the data collection was following a total count approach, which rarely includes observation-process covariates. We used the number of rangers as an offset to indirectly account for a respective bias. Future research based on ranger-collected data would benefit from the inclusion of observation process data, such as observation time, survey duration, and observers (Soofi et al. 2022a, Soofi et al. 2022b).Moreover, potential bird movements among wetlands contribute to variations in population abundance and richness, which we attempted to account for by using random effect intercepts and site-level random effect in the model. Lastly, conditions along migratory routes may also be an important factor influencing waterbird abundance, but due to the lack of available data, we were unable to include this in our analysis and thereby we reflected it as a limitation of our study.

5. Conclusion

Our study has several implications for the implementation of waterbird conservation. We demonstrate the significant and negative

effects of drought on the overall richness of waterbirds; with a decline in one unit of SPI resulting into an average decrease of three waterbird species per wetland. We also found that increases in water retained behind dams intensified this decline in waterbird richness by retaining water and reducing water flow to downstream wetlands. E.g. an average increase of 25 km^2 of water behind dams may lead to an average decrease of three species per wetland downstream. In arid and semi-arid regions like Iran, where prolonged droughts are increasingly frequent (Mirakbari and Ebrahimi-Khusfi, 2021), extensive dam construction poses a serious threat to waterbirds. For example, the key wetlands for migratory birds in Iran such as Ormia Lake and Gavkhoniare are alarmingly shrinking, partly due to persistent droughts and unsustainable water management practices (Rahimi et al., 2023; Shariati and Hemami, 2024). Additionally, our findings show the negative impact of frost days on the abundance of overall abundance. Variation in frost days may lead to further wetland habitat degradation by making habitats inaccessible for birds through freezing water surfaces and forcing birds to seek alternative foraging areas, in particular for wading bird species and fish-invertebrate feeders which are dependent on water surfaces for foraging. Our guild-specific analysis has shown the negative impact of frost days on the richness of wading birds and fish-invertebrate feeders due to limited foraging access. Rainfall influences the richness of bird guilds in various ways; while it benefits some guilds, it negatively impacts ground-gleaners by reducing suitable grassland habitats. Reed-dwellers benefit from increased rainfall and vegetation cover, highlighting the necessity of preserving surrounding vegetation for their habitats. Additionally, our results showed that the abundance of ground-gleaners, reed-dwellers, omnivorous birds, and fish-invertebrate feeders was positively associated with the SPI. Wet periods positively influence the abundance of reed-dwellers but can disrupt habitats if waterlogged conditions become excessive. We also found that ground-gleaners benefit from expanding wetland water surfaces but their persistence depends on both sufficient wetland water bodies and vegetation covers for foraging and resting. These results suggest that maintaining a balance between water surface and vegetation cover is critical for preserving this waterbird guild. Fish-invertebrate feeder abundance in wetlands was negatively affected by increasing water surface area behind dams upstream. Therefore, our results suggest sustainable management of water resources around wetlands to prioritize water allocation and maintain the natural flow of rivers feeding into wetlands. This approach is particularly essential for the conservation of waterbirds abundance and richness in arid regions, where the frequency of droughts threaten the abundance and richness of waterbirds.

CRediT authorship contribution statement

Shirko Shokri: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Mahmoud-Reza Hemami:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Mohsen Ahmadi:** Writing – review & editing, Methodology, Conceptualization. **Saeid Pourmanafi:** Writing – review & editing, Methodology. **Tejas Bhagwat:** Writing – review & editing, Methodology. **Johannes Kamp:** Writing – original draft, Validation. **Matthias Waltert:** Writing – review & editing, Validation, Supervision. **Mahmood Soofi:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

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.jnc.2025.127150.

Data availability

Data will be made available on request.

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