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# Drought-induced changes in hydrological and phenological interactions modulate waterbird habitats dynamics

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ABSTRACT

Floodplain wetlands are essential for the survival and reproduction of waterbirds, but droughts can negatively impact their food availability and habitat conditions, leading to a decline in waterbird abundance and diversity. To better understand the impact of hydrological and phenological variables on floodplain waterbird habitats during drought conditions, we employed hydrological modeling and remote sensing techniques to calculate fine-scale environmental variables. We constructed habitat suitability models using nine years of field surveys of waterbirds and identified the impact of the interaction effects between hydrological and phenological variables on waterbirds under drought and non-drought conditions. The results showed that hydrological and phenological variables can provide useful information for quantifying the habitat suitability of waterbirds. Drought-induced early water recession negatively impacted the quality of waterbird habitats, reducing their habitat suitability. Sedge eaters exhibited the most significant reduction of 34.47% in the total area of the lake, followed by seed eaters, fish eaters and invertebrate eaters. Tuber eaters had the largest increasing trend, with a significant increase area of 7.44% in total area. Our findings suggest that various feeding guilds exhibit distinct interactions in response to drought, which can be strengthened or weakened by alterations resulting from drought. For sedge eaters, seed eaters, and fish eaters, drought could result in a faster decline in habitat suitability by strengthening the interaction effects between variables. In contrast, for invertebrate eaters and tuber eaters, drought could weaken interaction effects between variables, resulting in a slower decline in habitat quality. The results provide valuable insights into the spatial distribution of overwintering waterbirds and can inform conservation efforts in wetlands.

## 1. Introduction

Floodplain wetlands play an integral role in the migration of waterbirds (Wang et al., 2020). They provide significant volumes of overwintering habitat and food, which is beneficial to the survival and reproduction of waterbirds (Wang et al., 2013). Unfortunately, due to the increase in anthropogenic activities and extreme climatic events, food richness and available habitat conditions for waterbirds continue to deteriorate. This has led to a continuous decrease in waterbirds abundance and richness (Aharon-Rotman et al., 2017; Pickett et al., 2018). In particular, drought events are becoming increasingly frequent, further exacerbating this threat and contributing to the degradation of waterbird habitats.

Drought-induced changes in hydrology and phenology are the primary drivers of the decline in waterbird habitat quality in floodplain wetlands. Early exposure to wetlands may advance the growth of

*Abbreviations:* AICc, Corrected Akaike Information Criterion; AUC, Area Under Curve; NSE, Nash-Sutcliffe efficiency coefficient; EOS, End time of the season; GLMM, Generalized linear mixed model; HSI, Habitat suitability index; LOS, Length of the season; LV, Largest data value for the fitted function during the season; MOS, Time for the mid of the season; NDVI, Normalized difference vegetation index; $R^2$, Coefficient of determination; RI, Receding interval between the start of water recession and the arrival of waterbirds; ROD, Rate of decrease at the end of the season; SA30, Average speed after 30 days of receding in Dongting lake; SB30, Average speed before 30 days of receding in Dongting lake; SOS, Start time of the season; VSOS, Value for the start of the season; WA30, Average water depth after 30 days of receding in Dongting lake; WB30, Average water depth before 30 days of receding in Dongting lake.

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vegetation, resulting in increased fiber content and decreased nitrogen content (Stejskalova et al., 2013). These nutritional changes can affect the food quality and digestion of waterbirds, which may threaten their survival and reproduction (Berner et al., 2005; Mueller et al., 2008; Veloso and Bozinovic, 1993). Therefore, it is critical to understand the impact of variables and response characteristics on floodplain waterbird habitats during drought conditions (Li et al., 2022), to improve conservation management.

Environmental variables can be used to describe changes in response to drought, and can be classified as either large-scale or fine-scale variables. Large-scale variables describe the average value of the entire habitat patch or the average value over several years. However, it's important to consider that they may not capture all response patterns and could result in biased conclusions (Row et al., 2022). Many studies (Doherty et al., 2016; Donnelly et al., 2022; Fedy et al., 2014) only considered large-scale environmental variables such as water level, flow at the outlet of Dongting Lake, and regional average normalized difference vegetation index (NDVI) values, neglecting the spatial heterogeneity within different regions of the lake. Moreover, the results may also be affected by temporal heterogeneity. Analyzing drought years and non-drought years together may obscure important results. For instance, prolonged drought in floodplain wetlands can lead to changes in waterbirds distribution (Wen et al., 2016), reduced reproducing and migration (Anderson et al., 2021), potentially leading to functional wetland loss and posing extinction risks to waterbird populations (Donnelly et al., 2022). Compared to large-scale variables, fine-scale environmental variables provide more accurate and detailed information for waterbird habitats (Wang et al., 2021). It has been found that higher resolution data can better explain the distribution of waterbirds, and researchers recommend a resolution that is sufficient to capture the smallest patches of suitable habitat for a given species' presence when conducting habitat suitability and distribution modeling (Šímová et al., 2019). Fine-scale environmental variables of wetlands can be obtained using hydrological modeling and remote sensing techniques, which can provide spatial accuracies ranging from 30 m to 1000 m. (Zhu et al., 2021) demonstrated that employing fine-scale hydrological and landscape variables in habitat suitability model effectively identifies potentially suitable habitats. However, research on the impacts of fine-scale hydrological and phenological variables on waterbird habitat suitability is limited.

The potential impacts of drought-induced hydrological and phenological changes on waterbirds may not simply be superimposed. Instead, the intricate interrelationships between these factors could trigger interactive effects. Prior research found that flood recession time had adverse effects on *Carex* emergence, inundation duration, and growth in floodplain wetlands (Guan et al., 2016; Yuan et al., 2019). Chen et al. (2015) found that *Carex* plants grew faster in plots with shorter inundation duration than in those with longer. Multiple variables could either amplify or attenuate their influence on waterbirds through these interactive effects. For example, delayed *Carex* emergence resulting from later water recession can benefit waterbirds by providing fresher food that enhances their digestion and energy conversion. However, later water recession can also limit waterbirds' foraging area due to higher water levels, resulting in the loss of access to sheltered habitats (Wang et al., 2013).

The Geodetector model (Wang et al., 2010) is a spatial statistical method that can quantify the influence of factors on a particular phenomenon by calculating the q-statistic. The Geodetector model is widely used in wetland ecosystem health studies (Yao et al., 2022) due to its simplicity and flexibility, which circumvents the limitations of traditional linear statistical methods that require intricate parameter settings. This model could also help researchers better understand the interaction mechanisms of independent variables. However, its potential for exploring the interactive effects of environmental variables on waterbird habitats has not been fully studied.

Dongting Lake is a Ramsar site in the Global 200 list of the most biologically valuable ecoregions (Yuan et al., 2015). Every year, numerous waterbirds stop at Dongting Lake temporally while migrating in large groups to their wintering grounds in Australia. In this study, we aim to identify the effect of drought on waterbird habitats through changes in hydrologic and phenological variables. Specifically, we aim to (a) determine the key environmental variables that affect the habitat suitability of waterbirds with different feeding guilds, (b) identify changes and trends in the habitat suitability of waterbirds in the entire lake area for drought and non-drought years, and (c) examine the effects of drought and non-drought years on the interaction between hydrological and phenological variables, and their impact on waterbirds.

## 2. Data and methods

### 2.1. Study area

Dongting Lake (28°59′–29°38′ N, 112°43′–113°15′ E) is located in the middle reaches of the Yangtze River (Fig. 1a). It is the second largest freshwater lake in China, with an area of 2625 $km^2$ and a total volume of 16.7 billion $km^3$. Owing to its unique geography and climate, Dongting Lake is a crucial habitat for wintering migratory birds in East Asia and is irreplaceable in terms of international biodiversity conservation status. Dongting Lake can be subdivided into three main regions: East, West, and South Dongting Lake (Fig. 1c). During the flood season (April to September), Dongting Lake is nearly entirely submerged with water levels ranging from 22.25 to 33.32 m. In contrast, during the dry season (October to March of the following year), the water level recedes, exposing vast mudflats and grasslands, and the water levels range from 20.13 to 29.77 m (Liang et al., 2021). This flooding pattern creates a favorable space for vegetation growth and waterbird habitat, making Dongting Lake an indispensable wintering ground for waterbirds. Numerous waterbird species start arriving at Dongting Lake from October and stay until March (Cao et al., 2008).

### 2.2. Waterbirds surveys

Empirical evidences indicate that there are significant fluctuations in the quantities and spatial distributions of waterbirds in Dongting Lake at the start and end of the overwintering season (Zhang et al., 2016). The waterbird population reaches its peak between December and January and remains stable, offering valuable insights into the spatial distribution of overwintering waterbirds in Dongting Lake, which is better correlated with environmental variables. In order to avoid repeat counting, surveyors are systematically segregated into nine groups to carry out a simultaneous survey. Field surveys of waterbirds were carried out in the first half of January from 2006 to 2014 by experienced surveyors using 10 × 42 binoculars and 20 × to 60 × spotting scopes along fixed line transects (Zou et al., 2017). Waterbird records were categorized into five feeding guilds based on their predominant foraging habits (Table S1), including tuber eaters, sedge eaters, seed eaters, fish eaters, and invertebrate eaters (Zhang et al., 2016). Some waterbird species exhibited multiple foraging habits, and these were grouped according to their primary foraging behaviors. The waterbirds recorded in January 2006 were assumed to have been influenced by environmental variables in 2005. Therefore, the corresponding year for environmental variables in the build habitat suitability models was set as 2005, and this approach was followed for subsequent years.

### 2.3. Environmental variables

#### 2.3.1. Hydrological variables calculation

We selected eight hydrological variables that were found to significantly impact the waterbirds' habitat suitability to create models that accounted for delayed hydrological changes (Jia et al., 2019; Zhang et al., 2018; Zhang et al., 2021b). These variables include RI, RD, SB30, SA30, WB30, WA30, SR, and WR (Table S2).

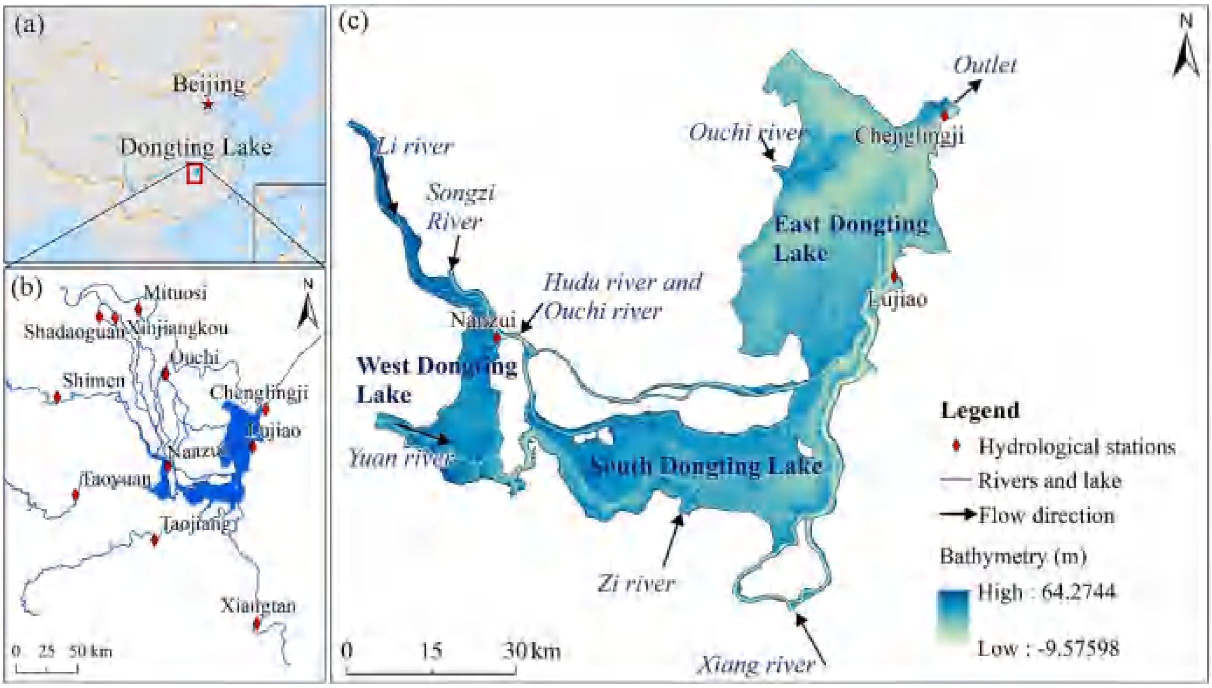


**Fig. 1.** (a) The geographical location of Dongting Lake in China; (b) Water bodies around Dongting Lake; (c) Underwater topography of Dongting Lake.

To calculate hydrological variables in the waterbird habitat of Dongting Lake, we utilized MIKE21 hydrodynamic model (Group, 2012) which provided daily water depth and flow velocity data across the entire Dongting Lake (Yang et al., 2019). The underwater topographic data of Dongting Lake in 2011 determined the lake bottom topography at a scale of 1:5000. Furthermore, the water flows from four major rivers (Xiang, Zi, Yuan, and Li) and three tributaries (Songzi, Hudu, and Ouchi) of the Yangtze River were used as upper boundary conditions (Fig. 1c), whereas the water level at the Chenglingji hydrographic station (the outlet of Dongting Lake) served as the lower boundary condition (Fig. 1b). Hydrological data was download from Hunan Hydrological Network (https://yzt.hnswkcj.com:9090). To assess the validity of the model, we compared simulated and observed water levels at Lujiao and Nanzui hydrological stations from January 1, 2005, to December 31, 2013. Model validation results indicated a consistent Nash-Sutcliffe efficiency coefficient (NSE) of 0.684–0.870 and coefficient of determination ($R^2$) of 0.780–0.899 throughout the study period, signifying compliance with the observations. Detailed model information can be found in Fig. S1.

### 2.3.2. Phenological variables calculation

We identified and extracted a total of 13 phenological variables (Table S2) that are potentially related to waterbirds using the MOD09Q1 dataset (Surface Reflectance 8-day L3 Global 250 m) available on the Google Earth Engine platform (https://earthengine.google.com/). This dataset includes the calculation of global surface reflectance every 8 days. For our analysis, we extracted 250 m Surface Reflectance Band 1 (620–670 nm) and 250 m Surface Reflectance Band 2 (841–876 nm) to calculate the NDVI value of the study area (Wang et al., 2019). Our data analysis period spanned from 2005 to 2013. The NDVI time series were smoothed by applying a Savitzky-Golay filter before being used in TIMESAT 3.3 software (Jonsson and Eklundh, 2004) to extract the phenological variables (Huang et al., 2022).

## 2.4. Habitat suitability model

We employed an optimized model selection process to determine the most appropriate Generalized linear mixed model (GLMM) and subsequently quantified the effects of hydrological and phenological drivers on waterbirds habitats dynamics. Finally, we used the best-fitted model to build the habitat suitability.

### 2.4.1. Model selection

We tested for and quantified the effects of hydrological and phenological drivers on waterbirds population dynamics using the GLMM. And we included survey year as a random effect. These analyses were implemented using the “glmer” function in the “lme4” package (Aharon-Rotman et al., 2017; Bates et al., 2015). Additionally, we eliminated explanatory variables that exceeded a variance inflation factor (VIF) value of 5, thereby confirming the absence of collinearity among the predictor variables. To specify the most appropriate GLMM model, we employed a backward stepwise strategy (Guan et al., 2016). We compared all possible models based on the corrected Akaike Information Criterion (AICc), and the models with the lowest AICc were selected. We used the “dredge” function in the MuMIn package (Barton, 2022; Team, 2022) in R to run a complete set of models with all possible combinations. Following Burnham and Anderson (2002), a model with $\Delta$AICc $<$ 2 was considered to have effectively equivalent levels of support, and we kept the most parsimonious model for further analysis. Additionally, we used “effectsize” (Ben-Shachar et al., 2020) and “glmm.hp” R package (Lai et al., 2022) to analyze the effect size and significance of environmental variables to habitat suitability models.

### 2.4.2. Model build and validation

We used all variables selected in the GLMM models as explanatory variables for habitat suitability models, which can be represented by the following equation (Liu et al., 2017):

$$HSI_i = logit[P(y_i|\gamma_i)] = x_j^T\beta + \gamma_i \tag{1}$$

where *HSI* is the habitat suitability index of waterbirds in feeding guild *i*, $y_i$ is the observation of the waterbirds in feeding guild *i*, $x_j^T$ is a column vector of environmental variables for this feeding guild, $\beta$ represents the fixed-effect model parameters, $\gamma_i$ is the random effect of group *i*.

We used the “predict” function in R to estimate the habitat suitability for all feeding guilds of waterbirds. All input data are processed at a resolution of 250 m. These predicted results were then converted to "TIF" format to analyze the changing trends of the HSI. It is common to require not only species distribution data but also species non-distribution data or background point data. However, in the process of constructing habitat suitability models, determining the method, quantity, and selection of pseudo-absence points poses a challenge (Warren et al., 2019). In our study, we adopted a methodology inspired by Row et al. (2022) to select pseudo-absence points. These pseudo-absence points were generated across the study region using a kernel density function. To ensure comparability, we matched the number of pseudo-absence locations in each year to the number of observed locations (Hysen et al., 2022). The validation was performed using AUC (Area Under Curve) estimates calculated from the observed and pseudo-absence points. We calculated the AUC values using the "pROC" package (Robin et al., 2011). An AUC value greater than 0.7 indicates acceptable predictive discrimination.

### 2.5. *Interaction effects analyses*

We conducted two analyses to evaluate how the interaction effects of environmental variables affected habitat suitability. The first analysis involved using trend analysis to assess the changing trend of habitat suitability. The second analysis involved using geographic detector models to evaluate changes in the interaction effects between environmental variables during drought and non-drought years.

#### 2.5.1. *Trend analysis*

To test our hypothesis that drought-induced changes in the timing of water recession significantly impacted habitat suitability, we constructed a multidimensional series of HSI data based on the timing of water recession. We used the Sen trend analysis (Şen, 2012) and MK test (Kendall, 1948) to examine the trend of changes in waterbird habitat suitability associated in changes at the start of water recession. The calculation method is:

$$S = \mathrm{Median}\left(\frac{x_j - x_i}{j - i}\right), \forall j > i \quad (2)$$

Where: $i$ and j represent different water recession times before and after, and x represents the HSI value of the pixel. Median represents taking the median of all results. S indicates the result of the trend analysis ($S > 0$ for an increasing trend, and $S < 0$ for a decreasing trend).

We use the test statistic Z for trend testing in MK test analysis (Kundzewicz et al., 2005), and when the absolute value of Z is > 1.96, the trend passes the significance test with 95% confidence.

#### 2.5.2. *Interaction effect analysis*

We employed Geodetector model to investigate the interactive effects of hydrological and phenological variables on the HSI of waterbirds during drought and non-drought conditions (Wang et al., 2010). Geodetector model is a useful tool for detecting and quantifying interactions between two factors, as well as the strength, direction, and linearity of the interaction. The q value calculated by the Geodetector model represents the proportion of the variation in the response variable that can be explained by a given environmental variable or a combination of variables (Wang et al., 2016). The $q$ value calculation formulas are as follows:

$$q = 1 - \frac{SSW}{SST} \quad (3)$$

$$SSW = \sum_{i=1}^{L} N_i \sigma_i^2, SST = N\sigma^2 \quad (4)$$

where $q$ represents the explanatory power of dependent variable Y to discretized independent variable X, $i$ represents the stratum, i.e., classification or zoning of X; $N_i$ and $N$ represent the number of units in stratum $i$ and the entire region respectively; $\sigma_i^2$ and $\sigma^2$ represent the variance of Y in stratum h and the entire region respectively.

By comparing the $q$ values of each variable individually and in combination, we were able to identify five types of interaction: non-linear enhanced, bi-enhanced, uni-weakened, non-linear weakened, and independent (Table S3). We compared changes in the interaction effect between drought and non-drought years. According to meteorological data and historical research (Wang et al., 2022), we defined 2006 and 2011 as drought years and other years as non-drought years.

## 3. Results

### 3.1. *Waterbirds abundance*

Based on the waterbirds surveys results, a total of 900,748 waterbirds were recorded in Dongting Lake during the study period (2005–2013). Among them, the most abundant waterbird species were sedge eaters, while the least abundant were tuber eaters. The drought year of 2006 witnessed the lowest waterbird population of 46,336 individuals. Detailed summaries of the waterbird species can be found in Table S1 and Fig. S2.

### 3.2. *Hydrological and phenological conditions*

The results showed that water recession began earlier than November 10th in all years (Fig. 2 and Table S4). The earliest water recession occurred in 2006, 85 days before waterbirds' arrival, while the latest was in 2005, only 7 days before their arrival. The duration of the water recession was the longest in 2006 and 2011, with 299 and 238 days respectively. In Dongting Lake, SOS of vegetation (Fig. S3) was split into two types: SOS less than 132 days was dominated by *Phragmites*, while SOS greater than 132 days was dominated by *Carex* and *Phalaris*. We found a significant correlation between the start time of water recession and phenological variables in pixels with SOS greater than 132 days (Fig. 2). The results of the correlation analysis between the median statistical values of phenological variables and the start time of water recession show that SOS and MOS are positively correlated with the time of water recession (SOS: Pearson's correlation coefficient = 0.80, $p < 0.01$; MOS: Pearson's correlation coefficient = 0.78, $p < 0.05$), while LOS is negatively correlated with the time of water recession (LOS: Pearson's correlation coefficient = -0.80, $p < 0.01$).

### 3.3. *Model selection and validation*

Table S5 presents GLMM model selection results. Each model incorporates at least one hydrological and phenological variable, as shown by the standardized variable coefficients of GLMMs (Fig. 3 and Fig. S4). This consistent occurrence highlights the critical role of hydrological and phenological variables and their joint influence on all species. Phenological variables, such as SOS and MOS, calculated in terms of Julian day, have a positive effect on waterbirds. This finding is consistent with Zhang et al. (2021a), which suggest that delayed vegetation growth seasons have a positive impact on waterbirds. Additionally, the same environmental variables have similar impacts on different foraging guilds. For example, ROD affected both sedge eaters and tuber eaters negatively, and WB30 affected both seed eaters and invertebrate eaters positively, to varying degrees.

The AUC values of selected GLMM models varied across five feeding guilds (Fig. S5). The range of these values was between 0.769 and 0.840. The model achieved the highest AUC value of 0.840 for the models of invertebrate eaters, indicating its strong performance in predicting habitat suitability. On the other hand, the models of tuber eaters had the lowest AUC value of 0.769. However, all models scored higher than 0.700, indicating satisfactory performance across all models.

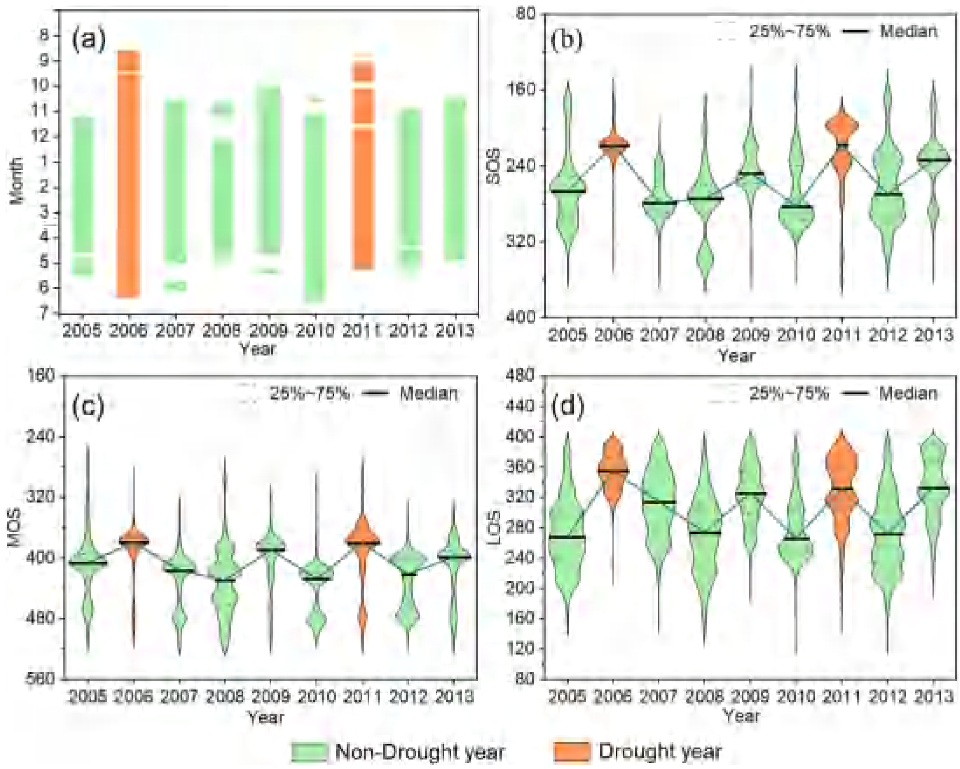


**Fig. 2.** (a) Temporal changes of water recession days, August to December represents the month of the corresponding year, and January to July represents the data of the following year. Water recession was calculated from the duration when the water level of Chenglingji gauging station was lower than 25.3 m. (b) ~ (d) SOS, MOS and LOS for the area of SOS greater than 132 in 2005–2013.

### 3.4. Change of habitat suitability

The annual average HSI predictions for five feeding guilds in Dongting Lake were shown in Fig. 4. The results revealed that sedge and seed eaters in East Dongting Lake had a significantly higher HSI value compared to those in West and South Dongting Lake (Wilcoxon test, $p < 0.05$). However, there was no significant difference in habitat suitability between West and South Dongting Lake (Wilcoxon test, $p = 0.55$). Similarly, fish and invertebrate eaters also had a higher HSI value in East Dongting Lake (Wilcoxon test, $p < 0.05$), but South Dongting Lake was more suitable for these feeding guilds compared to West Dongting Lake (Wilcoxon test, $p < 0.05$). Tuber eaters exhibited the highest habitat suitability in South Dongting Lake, with an average of 4.66, while East and West Dongting Lake had lower habitat suitability for this feeding guild (Wilcoxon test, $p < 0.05$). Significantly, habitat suitability for waterbirds was 0.69 lower in 2006 and 2011 than in other years (Wilcoxon test, $p < 0.05$) due to drought. The area where *Carex* and *Phalaris* grow on the floodplain wetland formed after water recession is preferred by all waterbirds and has a higher habitat suitability value. The habitat suitability for various feeding guilds across the entire Dongting Lake is shown in Fig. S6 to S10.

The impact of earlier water recession times on the quality of habitat for sedge eaters is significant, resulting in a reduction of 34.47% of their total area (Fig. 5, Table S6). As the start of the water recession advanced, there was a corresponding decrease in HSI, with a daily change trend of $-0.0198\ d^{-1}$. A declining trend was also observed for seed eaters and fish eaters, with change trends of $-0.0115\ d^{-1}$ and $-0.0083\ d^{-1}$, respectively. Tuber eaters showed the largest increasing area, with the significantly increased area accounting for 7.44% of the total area and a changing trend of $-0.0011\ d^{-1}$. Invertebrate eaters were affected insignificantly with a changing trend of $-0.0038\ d^{-1}$. Furthermore, the area of increased HSI for waterbirds during the dry season corresponded to areas of former low HSI. This suggests that waterbirds may migrate to the alternative area such as deeper water or areas with increased human activity.

### 3.5. Interaction effect of variables

The interaction effects between hydrology and phenology are mainly non-linear enhanced (Table S7). This indicates that the combined effect of these factors is greater than their individual effects. Consequently, the changes in HSI will be more significant when the interaction effects are considered, compared to scenarios where the effects are considered independently. Environmental variables influenced by drought can reduce habitat quality, and the interaction effects of drought can either strengthen or weaken this impact, depending on the feeding guilds (Fig. 6). The feeding guilds can be categorized into two groups (Fig. 7). For sedge eaters, seed eaters and fish eaters, most of the interaction effects are strengthened in the presence of drought. In contrast, for tuber eaters and invertebrate eaters, the interaction effects weaken with drought. Although the change in the interactive effects for tuber eaters, fish eaters, and invertebrate eaters between drought and non-drought periods is not significant, their changing trends can be inferred from their median and mean values.

## 4. Discussion

Changes in water level fluctuations due to drought will affect exposure and nutrient cycling in semi-permanently flooded areas, leading to changes in the habitat characteristics of waterbirds such as available habitat area, habitat heterogeneity, and species abundance (Dai et al., 2020). Recent studies have pointed out that a longer interval between the start of water recession and the arrival of waterbirds (measured by the RI value) results in lower habitat quality for the waterbirds, which means more harmful to them (Wei and Zhou, 2023). Firstly, in drought years, the longer growing period of the vegetation leads to taller sward

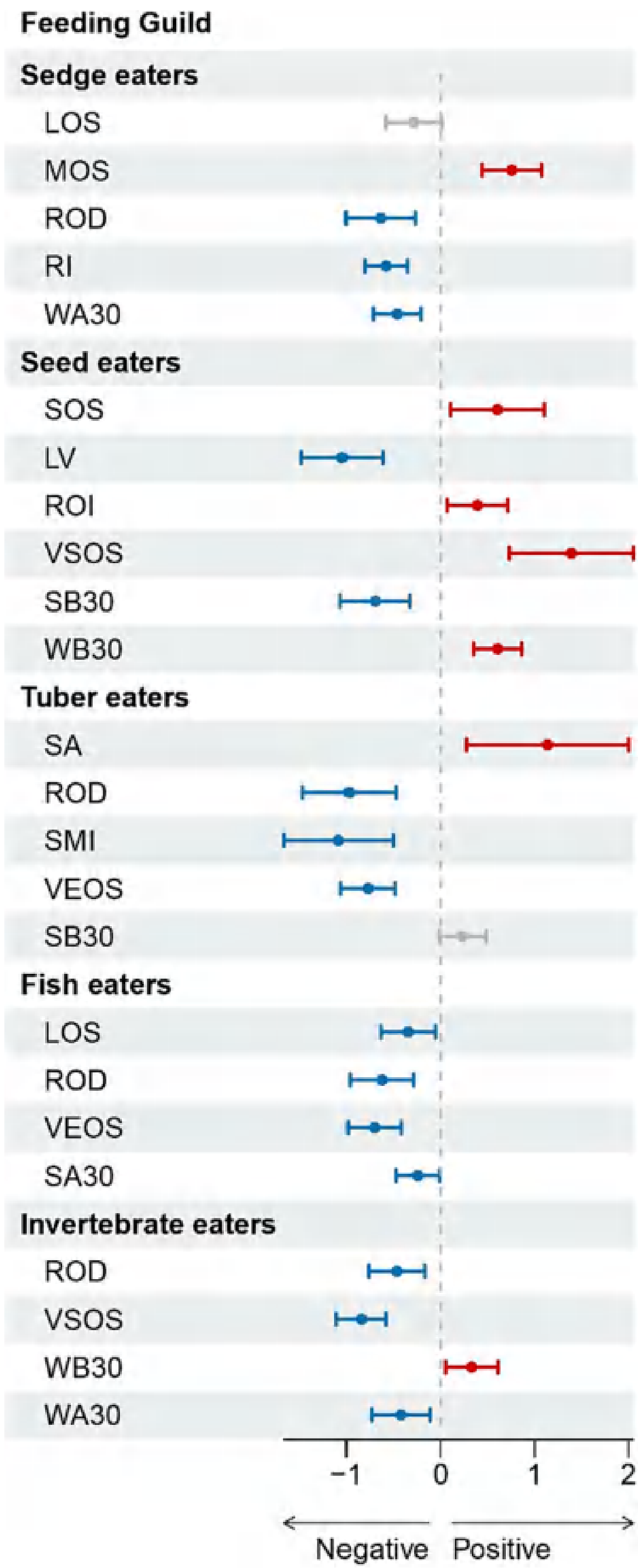


**Fig. 3.** Mean and 95% CI for standardized variable coefficients of GLMMs. The red lines indicate the significant positive effects (p-value $<$ 0.05), the blue lines indicate the significant negative effects (p-value $<$ 0.05), and the grey lines indicate the effects are not significant (p-value $>$ 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

height and higher fiber content (Durant et al., 2004), resulting in lower energy value of the vegetation, and waterbirds cannot get positive energy feedback during the feeding process (Wang et al., 2013). Secondly, the moist mudflats dry out after a certain amount of exposure, preventing the waterbird's beak from penetrating the soil for food (Aharon-Rotman et al., 2017). These changes are further influenced by the hydrological conditions before and after the water recession. Deeper water depths before the water recession and more shallow water depths after the water recession, as measured by WB30 and WA30 respectively, positively correlate with higher habitat suitability for waterbirds (Fig. 3). This can be explained by a high water level before the water recession and fast recession velocity, which provides more areas of available food resources for waterbirds throughout the season. And the impact of flow velocity on waterbirds has always been negative, as measured by SA30 and SB30. The slow flow velocity maintains moist conditions on the surface, supporting feeding by waterbirds and promoting the growth of *Carex* and other vegetation communities (Zhang et al., 2021a).

Changes in phenological variables caused by drought also affect waterbirds. We use phenological variables calculated by the NDVI index to reflect changes in vegetation growth in habitats (Boelman et al., 2003). Premature vegetation growth hinders waterbirds while excessive growth upon their arrival constrains their distribution. This is because earlier water recession times will lead to earlier start times of vegetation growth, and make the NDVI significantly higher when waterbirds arrive, resulting in higher grassland height and higher fiber content. However, due to the size of waterbirds and their low digestive efficiency for mature vegetation, the vegetation under these conditions is not suitable for them to feed on (Durant et al., 2004; Wang et al., 2013). Therefore, the earlier occurrence of water recession in drought years makes the vegetation growth cycle advance, the food quantity of waterbirds may be higher and the food quality may be lower, thereby reducing the habitat quality. In addition, our research has found that some unobservable phenological variables are also included in the model. These variables provide important information about vegetation growth patterns, maturity stages, standing periods, and overall health, despite their subtle character and the challenges of direct calculation (Singh et al., 2022). Incorporating an appropriate set of phenological and hydrological variables can greatly enhance the accuracy of models aimed at capturing these nuances in their responses (Zhang et al., 2016).

Our analysis of interaction effects demonstrated that different waterbird groups exhibit distinct response patterns to the decline in habitat quality during drought periods, depending on their feeding guilds. Similar results have been also reported by (Zhang et al., 2023), they reported that species with different food sources have different requirements for hydrology and vegetation growth conditions. Impacts of drought-induced changes in hydrological and phenological interactions can be observed through three mechanisms: phenology-phenology interaction, hydrology-hydrology interaction, and phenology-hydrology interaction. Interaction effects between phenological variables are influenced by drought. The interaction effects between MOS and LOS in this research (Fig. 2) support the previous study that a later MOS generally leads to a longer LOS (Julien and Sobrino, 2009; Wu et al., 2016). Additionally, there is a significant negative correlation between SOS and LOS in a similar floodplain, which supports previous research that an earlier SOS results in a longer LOS (Huang et al., 2022; Jeong et al., 2011; Yu et al., 2017). Similarly, interaction effects between hydrological variables are also influenced by drought. Hydrological variables are sensitive to changes in temperature and precipitation, which can lead to interactions. When the water level in Dongting Lake is low, such as at Nanzui (<30 m) or Chenglingji (<27 m) (Huang et al., 2014), the monthly average water level is roughly proportional to the runoff into the lake. This implies that during the dry season, the water level at Dongting Lake is predominantly determined by the inflow of water into the lake. Temperature directly affects the development of hydrological drought in flooding wetland regions

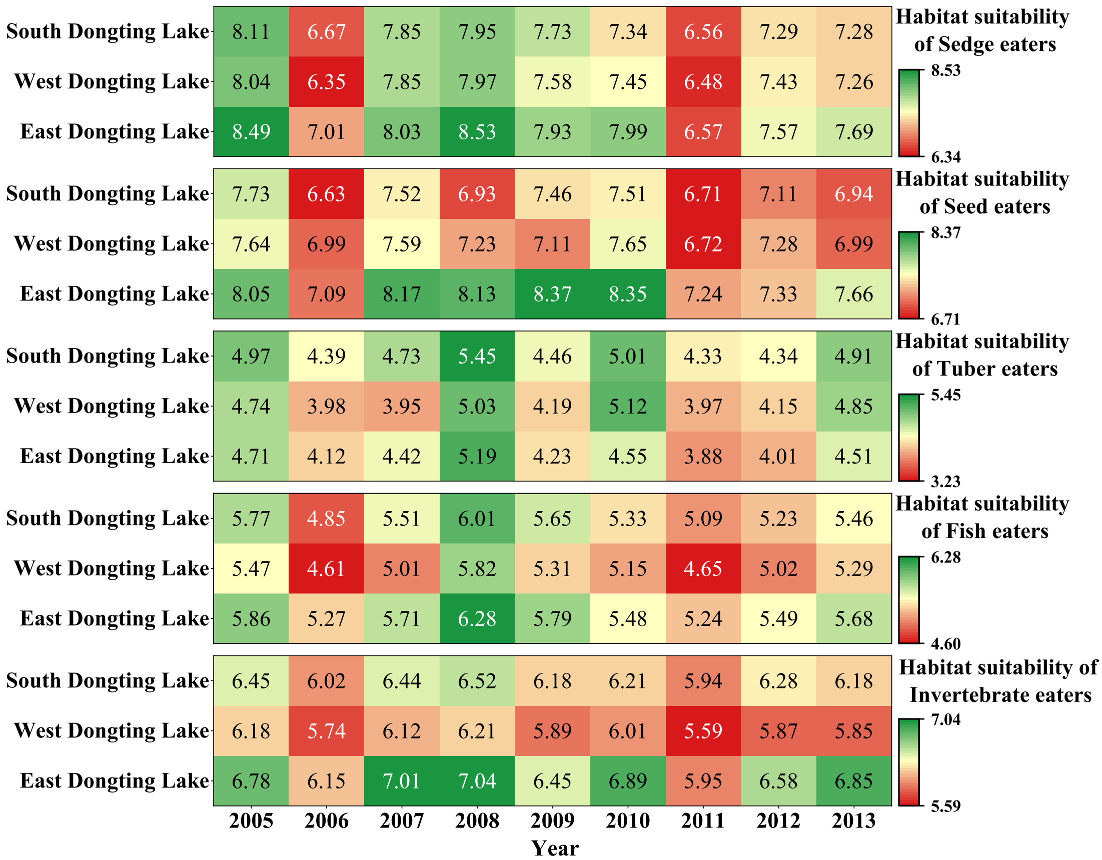


**Fig. 4.** Annual predictions of HSI for waterbirds in Dongting Lake.

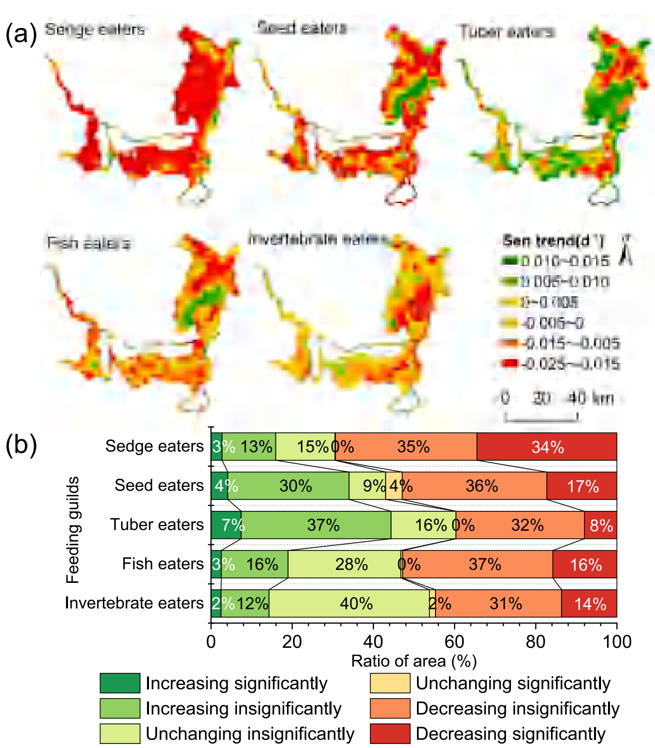


**Fig. 5.** (a) Changes in waterbirds habitat suitability with the advance of water recession time. (b) The result of MK test on waterbird HSI with changing habitat area.

(Pratap and Markonis, 2022), while precipitation, temperature, and vegetation cover change are all critical factors that affect the hydrologic response to extreme drought conditions (Konapala and Mishra, 2020). Lastly, drought affects phenology-hydrology interaction effects. In previous studies, the water recession time was found to be important in determining the timing of *Carex* growth in floodplain wetlands (Huang et al., 2022). Drought can rapidly reduce soil moisture and limit long-term water availability in wetlands, negatively impacting plant growth, production, and species richness (Thompson et al., 2009). The resulting reduction in groundwater levels and soil water availability may cause an increase in terrestrial plant species and a decline in species that are better adapted to wetland conditions (Herrera-Pantoja et al., 2012; Thompson et al., 2009). There was evidence of two types of lag effects due to altered hydrology after vegetation was transplanted from the wetter zone to the drier interior floodplain (Brotherton et al., 2019): a decline in survival and flowering over time, and constrained leaf and flower production. Which means that the impact of drought may continue to affect the next vegetation growth season.

The Chinese government has recently passed the “Yangtze River Protection Law” (Li and Jin, 2023), which emphasizes the significance of preserving the ecology of the Yangtze River. This has led to large investment by local authorities in the preservation and rejuvenation of wetland ecosystems in Dongting Lake over recent years. Nevertheless, an insufficient comprehension of the relationship between waterbirds and the environment could potentially create a disparity between scientific theory and practical application. Numerous studies have shown that wetland restoration could improve habitat quality for waterbirds by providing foraging, nesting, roosting habitats, and better food resources, among others (Oneal et al., 2008; Sebastián-González and Green, 2016). Building ecological dikes is one of the common restoration measures (Monfils et al., 2014). Studies have shown that dike wetlands can provide sufficient food resources to maintain high waterbird diversity by

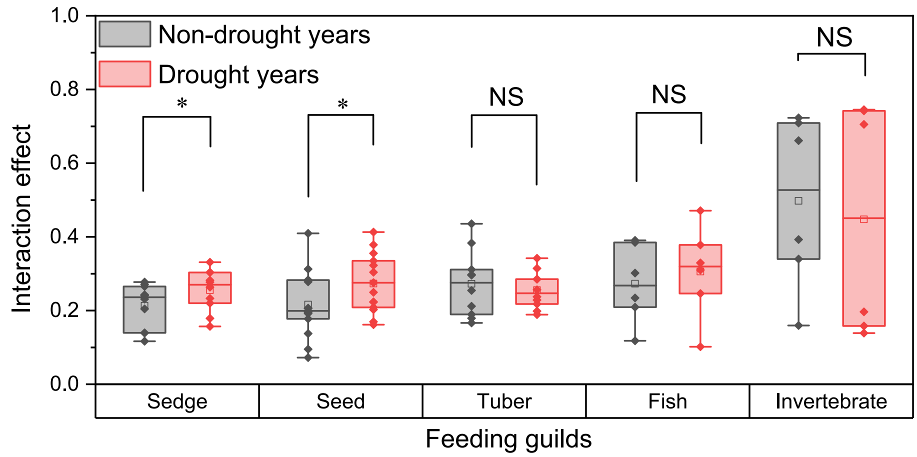


**Fig. 6.** Differences in the interaction effect of environmental variables between drought and non-drought seasons. "*" represented $p < 0.05$ (Wilcoxon test); NS represented not significant.

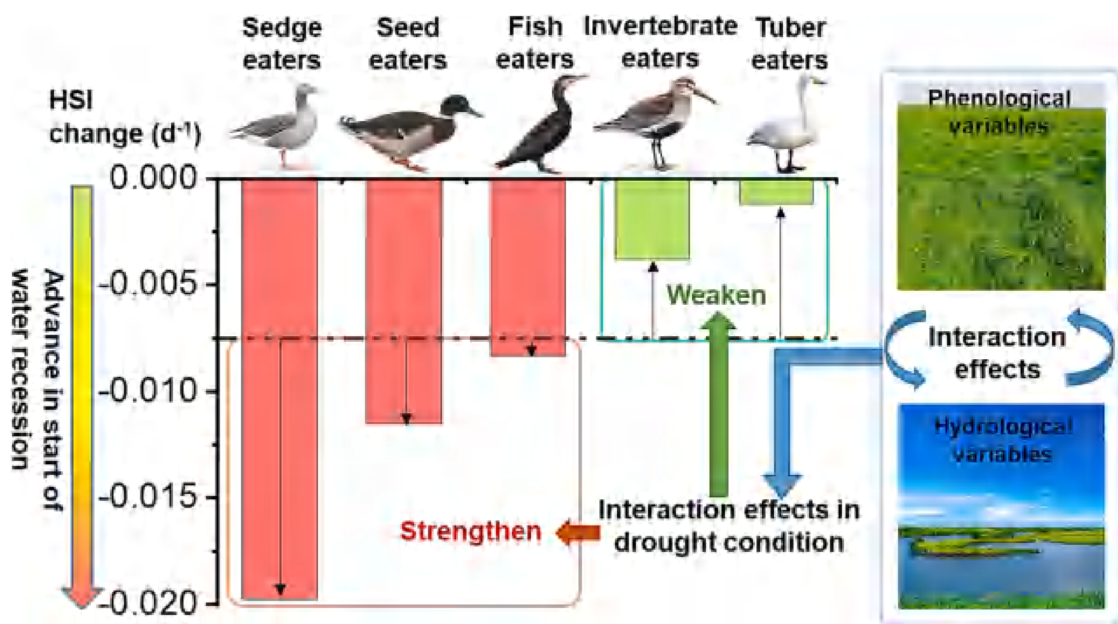


**Fig. 7.** The correlation between interaction effects and changing trends of HSI under drought conditions. Changing trends of HSI were calculated from Table S5. The dashed line is an auxiliary line for comparing the degree of decline in HSI, and the black arrow indicates the difference in HSI change of different species at the auxiliary line.

adjusting water levels (Murkin et al., 1982). However, in order to connect the hydraulic conditions of Dongting Lake and restore its natural characteristics, the government has demolished some dikes. A study evaluated the difference in waterbird diversity before and after the demolition (Zhu et al., 2022), and found that populations of all waterbird species except tuber eaters have significantly decreased, especially sedge eaters. This is similar to our research results. Although some dikes were previously used for commercial purposes, they have a potential negative impact on the hydrological connectivity of the area, and also on water quality. However, it is necessary to promptly take ecological restoration measures after the demolition of dikes in order to maintain the quantity and quality of waterbird habitats. We suggest controlling the timing of water recession in suitable areas, regularly adjusting water levels, and aligning the growth cycle of vegetation with the needs of waterbird populations. Given the varying interaction effects among different feeding guilds of waterbirds, those with stronger interactions may exhibit greater sensitivity to restoration measures. Consequently, the optimal location of wetland restoration efforts can be determined based on the specific needs of decision makers (Liang et al., 2018a; Liang et al., 2018b).

## 5. Conclusion

In this research, we investigated the impact of hydrological and phenological variables on waterbird habitats and used these variables to construct habitat suitability models. These models were used to identify the impact of the interaction effects between hydrological and phenological variables on waterbirds under drought and non-drought conditions. The results indicates that hydrological and phenological variables can reflect changes in waterbird habitats under different degrees of drought. Drought leads to a decline in the habitat suitability of waterbird habitats, but the degree of impact varies among different feeding guilds. The interaction effects between hydrology and phenology are greater than their individual effects, and the interaction effects of drought can either strengthen or weaken this impact, depending on the feeding guilds. As the severity and frequency of drought events continue to worsen due to climate change, it is increasingly important for policy makers to take measures to restore drought-affected waterbird habitats.

## CRediT authorship contribution statement

**Xiang Gao:** Methodology, Formal analysis, Writing – original draft. **Jie Liang:** Funding acquisition, Writing – review & editing. **Ziqian Zhu:** Data curation, Validation. **Weixiang Li:** Conceptualization, Methodology, Data curation. **Lan Lu:** Conceptualization, Methodology. **Xin Li:** Writing – review & editing. **Shuai Li:** Data curation, Validation. **Ning Tang:** Data curation, Validation. **Xiaodong Li:** Formal analysis.

## 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.

## Data availability

The authors do not have permission to share data.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2023.130228.

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