Crucial sites and environmental variables for wintering migratory waterbird population distributions in the natural wetlands in East Dongting Lake, China

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HIGHLIGHTS
• Waterbird populations were analyzed at community, foraging guild and species levels.
• Five crucial wintering sites were verified in East Dongting Lake.
• Six crucial environmental variables were identified in East Dongting Lake.
• Crucial sites and environmental variables were foraging guild-specific.
• Crucial sites and environmental variables were species-specific.

ABSTRACT
Dongting Lake is the second largest freshwater lake in China and is one of the globally important wintering sites for migratory waterbirds in the East Asian–Australasian Flyway. Crucial sites and environmental variables for wintering migratory waterbirds are of great concern in the Dongting Lake wetlands. In this research, based on annual (2003/2004–2016/2017) waterbird and habitat census data, we recognized the crucial sites for waterbirds during wintering seasons by comparing the difference of waterbird populations at the community, foraging guild and species levels in different natural wetlands within East Dongting Lake, and then identified the crucial environmental variables affecting waterbird distributions by analyzing the relationship between waterbird populations and the environmental variables, including vegetation area, mudflat area, water area with the depth of 0–20 cm, water area with the depth of 20–50 cm, water area with the depth of 50–100 cm, water area with the depth >100 cm, growth status of vegetation (Min, Mean and Max NDVI), and the human disturbance. Results indicated that five natural wetlands, i.e., Daxiaoxi, Chunfeng, Baihu lakes, Dingzi dyke and Tanjiawei, were recognized as the crucial wintering sites for migratory waterbirds in the East Dongting Lake. Among the ten selected environmental variables, water areas with the depth of 0–20 cm, 20–50 cm and >100 cm, human disturbance, Min and Mean NDVIs were identified as the crucial environmental variables overall. Waterbirds at different levels...
1. Introduction

Dongting Lake, the second largest freshwater lake in China, is a Ramsar site and also one of the eco-regions that listed in the Global 200 as the most crucial to the conservation of global biodiversity (Olson and Dinerstein, 1998). East Dongting Lake, the major part of Dongting Lake, has been recognized as the key wintering region in the East Asian–Australasian Flyway (Cao et al., 2008). The East Dongting Lake wetlands, however, were not used equally by waterbirds, e.g. geese (Wang et al., 2012; Zhang et al., 2018; Zou et al., 2017). Therefore, it is of critical importance to recognize the crucial sites for wintering migratory waterbirds in East Dongting Lake.

Waterbirds are key indicators of the quality and importance of wetlands (Erwin and Custer, 2000; Ogden et al., 2014; Olsson and Rogers, 2009; Wetland International, 2006). For the East Dongting Lake wetland, the wintering waterbirds are significant indicator of wetland biodiversity. The spatiotemporal population distributions of wintering waterbirds, undoubtedly, can be affected by variations in wetland habitat quality in the East Dongting Lake, e.g. hydrological regime, food availability, and human disturbance.

Under the background of climate change and the operation of the Three Gorge Dam, the hydrological regime in Yangtze River and Dongting Lake have suffered obvious changes (Dai et al., 2017; Lu et al., 2018; Xie et al., 2015; Yuan et al., 2015), and finally posing threats to ecosystem services (e.g. biodiversity maintenance) of the wetland (X. Wang et al., 2013a; Yuan et al., 2014; Zhang et al., 2016; Zhang et al., 2018; Zou et al., 2017). In East Dongting Lake, the mudflats and sedge meadow vegetation are served as crucial foraging habitats for wintering waterbirds. These habitats are closely related to hydrological regimes since they are exposed gradually with water recession in mid-autumn (Liu et al., 2006; Xie et al., 2015). In 2003, the full operation of the Three Gorges Dam (TGD) have dramatically changed the hydrological regimes and thus the physical habitats in East Dongting Lake (Sun et al., 2012; Xie and Chen, 2008; Xie et al., 2015). Water discharge or storage by the TGD may lead to too early or too late explosion of the sedge meadows and mudflats in East Dongting Lake wetland (Guan et al., 2014). Water depth is considered to be one of the most important factors influencing the habitat utilization by waterbirds because of the restrictions of bird morphology, such as the lengths of tarsometatarsi or necks (Isola et al., 2000; Ma et al., 2010). Drastic changes in hydrological regimes in particular the water level fluctuations might result in the changes of water depth, especially in wetlands with different elevations (topography). Yuan et al. (2014) reported that human disturbance was also a crucial environmental variable affecting the populations and distributions of waterbirds. In conclusion, hydrological regime, human disturbance, and in particular food availability, are important for waterbird populations and distributions, yet the crucial environmental variables affecting the spatiotemporal dynamics of waterbird populations in East Dongting Lake remains largely unexplored.

This study analyzes the relationships between the wintering waterbird populations and their wintering habitat in East Dongting Lake over the last decade (2003/2004–2016/2017) using remote sensing and geographic information system (GIS). Considering that mixed responses of avian community dynamics to environment changes are linked to avian guild composition and structure (Cueto and Lopez de Casenave, 2000; Y. Wang et al., 2013b), the waterbird populations in this study were analyzed in three different levels including the community, foraging guild, and species levels. We aimed to (1) recognize the crucial sites for waterbirds during wintering seasons by comparing the difference of waterbird populations at the community, foraging guild and species levels in different wetlands within East Dongting Lake, and (2) identify the crucial environmental variables for waterbird population distributions by analyzing the relationship between waterbird populations and the environmental variables. The results would provide potential insights into the conservation of waterbirds and their associated habitats in the Dongting Lake wetlands as well as in the middle Yangtze River floodplains.

2. Methods

2.1. Study area

Seven natural wetlands, i.e., Daxiaoxi lake, TANJIaweizi, Dingzi dyke, Junshanhou lake, Baihu lake, Hongqi lake, and Chunfeng lake, were selected as the study areas (Fig. 1), because these areas are overall the most important wintering habitats for migratory waterbirds within East Dongting Lake. The seven natural wetlands comprise approximately 15,610 ha (Daxiaoxi lake, 1400 ha; TANJIaweizi, 390 ha; Dingzi dyke, 2180 ha; Junshanhou lake 1580 ha; Baihu lake, 3510 ha; Hongqi lake, 2100 ha; Chunfeng lake, 4450 ha) and includes three major habitats, i.e., water, vegetation, and mudflat habitats. The vegetation habitats were exclusively dominated by sedge Carex spp. meadows. The seven natural wetlands are directly connected with the Yangtze River, hence the water level in the wetlands change along with the water level fluctuations in the Yangtze River.

Human disturbances are different in seven natural wetlands. Lower human disturbances occurred in Daxiaoxi and Baihu lakes, mainly due to the closed management in Daxiaoxi lake and hard reaching to Baihu lake that located in the hinterland of Dongting Lake. Dingzi dyke is near to road while fishing activities are relative common in Hongqi lake, hence the human disturbance were classified as moderate in these two sites. Reed harvesting and fishing occurred in TANJIaweizi and Chunfeng lake, respectively, while Junshanhou lake is near to Junshan park (tourist attraction), thus human disturbance was classified as higher in these three sites.

2.2. Waterbird surveys

Wintering waterbirds were surveyed in the seven natural wetlands during 2003/2004–2016/2017. Waterbird survey data during 2003/2004–2013/2014 were acquired from the management office of the East Dongting Lake Nature Reserve. Because most wintering waterbirds fly to East Dongting Lake in November and fly away in March, the peak population is present in January. Therefore, all surveys covered the study areas (Fig. 1) and were carried out during a 2–3-day period in January. Each survey started 1 h after sunrise and lasted 4–5 h every day. Two to three investigators counted wintering waterbird individuals using 10 × 42 binoculars and 20× to 60× spotting scopes by the direct counting method. We resurveyed waterbirds in the winters of 2014/2015–2016/2017 (January in 2015–2017) in the same areas as during the winters of 2003/2004–2013/2014 waterbird surveys. We used the same protocols as used for all surveys during 2003/2004–2013/2014.
Waterbird species diversity (SHDI), richness and density were used to evaluate the waterbird community composition pattern. Similar to Armitage et al. (2007), SHDI was calculated in the seven natural wetlands in the wintering seasons during 2003/2004–2016/2017, where $SHDI = -\sum (p_i)(\ln p_i)$ and $p_i$ is the proportion of waterbirds that belong to the $i$th species (Krebs, 1994). Due to the distinct feeding requirements of specific waterbird assemblages and according to their feeding habits (Y. Wang et al., 2013b; Wu et al., 2014; Zhang et al., 2016), the wintering waterbird species were aggregated into five foraging guilds, i.e., tuber feeders, herbivores, fish eater, invertebrate eaters and omnivores (Table 1). All the observed wintering waterbird species and their according guilds were listed in Appendix S1.

The East Dongting Lake wetlands are the major wintering regions for waterbirds in particular the threatened species. It might be more valuable to track the changes in the populations of dominant or threatened species and the relations to their corresponding habitat, and therefore for the conservations of waterbirds and the wetlands. Ten dominant or threatened species were chosen to analyze the waterbird-environment correlations at the species level. Ten species included Common crane, Tundra swan, Bean goose, Lesser white-fronted goose, Great cormorant, Grey heron, Eurasian Spoonbill, Dunlin, Falcated duck and Common teal (Appendix S2).

Given the different areas of seven study sites, densities of waterbirds at the foraging guild and species levels were used to analyze their population and distribution patterns as well as the species-environment correlations.

### 2.3. Environmental variables

Ten environmental variables were chosen in the seven natural wetlands to assess the influence of environment changes on waterbird population dynamics in the natural wetlands during 2003/2004–2016/2017. The variables are: vegetation area, mudflat area, water area with the depth of 0–20 cm, water area with the depth of 20–50 cm, water area with the depth of 50–100 cm, water area with the depth >100 cm, growth status of vegetation (Min, Mean and Max NDVI), and the human disturbance. The summary of all environmental variables and their ecological importance to wintering waterbird was provided in Appendix S3.

The area of water, mudflat, vegetation habitats in the seven natural wetlands were extracted using 16 satellite images (Appendix S4), i.e., one Landsat TM images, ten Landsat ETM+ images, four Landsat 8 OLI images, and one GoogleEarth image. Landsat ETM+ images have data gaps due to the Scan Line Corrector (SLC) failure since May 30, 2003. Gap Phase Estimator (provided by USGS) was used to calculate the approximate area from two Landsat ETM+ images (e.g. two Landsat images acquired on Jan. 27 and Feb. 5, 2004, Appendix S4) and thus filled the gaps of Landsat ETM+ images. The decision tree classification method was used for such habitat classification, according to the framework by Xie et al. (2015). The habitat classifications extracted from Landsat images (30 m resolution) were rectified by comparing them to the habitat classification extracted from the GoogleEarth image. Classification accuracy was evaluated using a standard error matrix.
The dataset used in this study was MODIS 16-day composite NDVI time series data products (MOD13Q1) during 2003/2004–2016/2017 provided by Earth Resources Observation Systems (EROS) data center, the United States Geological Survey (USGS), with the spatial resolution 250 m. The periods of data acquisition were from January 16–31 or February 1–16 according to the dates of waterbird surveys in each wintering season. The water area with the depth of 0–20 cm, 20–50 cm, 50–100 cm and >100 cm were extracted from the water area classifications with the water level (8:00 AM at Chenglingji Hydrological Gauging Station, Sun et al., 2012; Xie et al., 2015) minus the elevation. Specifically, firstly, based on the high resolution DEM (30 m resolution), the elevations of the water area was reclassified with a gradient of 0.1 m. Then, the water levels during the waterbird surveys were inquired from the website of Hunan Hydrological Information Inquiry System (http://www.hnhsww.com.cn/). Finally, water areas with the water depths of 0–20 cm, 20–50 cm, 50–100 cm and >100 cm were calculated by the water habitats with the elevation intervals (0–0.2 m, 0.2–0.5 m, 0.5–1 m, and >1 m) less than water level. For example, the water level was 22 m during the waterbird survey in 2016/2017, therefore, water areas with the water depths of 0–20 cm, 20–50 cm, 50–100 cm and >100 cm were the areas of the water habitats with the elevation intervals with 21.8–22 m, 21.5–21.8 m, 21–21.5 m, and <21.5 m, respectively. Human disturbances were ordinal data according to the human activities (Details were presented in the section of Study area), i.e., Daxiaoxi and Baihu lakes (1, lower human disturbance), Dingzi dyke and Hongqi lake (2, moderate human disturbance), Tanjiaweizi, Chunfeng and Junshanhou lakes (3, higher human disturbance).

2.4. Data analysis

The normality tests were used the methods of D’Agostino–Pearson omnibus test (D’Agostino et al., 1990), indicating that all waterbird and environmental variables passes normality tests (all p > 0.05).

The seven natural wetlands, however, might not be used equally by waterbirds at the community, foraging guild and species levels. At the community level, one-way ANOVAs were used to test whether there were significant differences in waterbird populations, i.e., the species number, the abundance (individuals of waterbirds), the density (individuals of waterbirds per hectare) and the diversity (SHDI), among the seven natural wetlands. If there were significant differences were observed in waterbird populations among these wetlands, post hoc tests (Games–Howell multiple comparison) were used to identify the crucial sites for waterbirds (significant higher waterbird populations in such sites than others). At the foraging guild and species levels, the densities of five foraging guilds and 10 threatened or dominant species were respectively used to represent the waterbird populations in the seven natural wetlands. The same protocols of one-way ANOVAs and post hoc tests were used to identify the crucial sites for waterbirds at the foraging guild and species levels.

Differences of environmental variables in the seven natural wetlands might be the probable reason leading to waterbird population distribution patterns in these wetlands. Thus, one-way ANOVAs and post hoc tests were also used to examine the differences of environmental variables in the seven natural wetlands. The protocols of one-way ANOVAs and post hoc tests were similar to those used in analyzing the differences of waterbird population distribution patterns in seven natural wetlands.

Forward stepwise linear regression or Gaussian regression analyses were then used to examine the relationships between the waterbird populations in the seven natural wetlands and the corresponding environmental variables at the community, foraging guild and species levels, respectively. The crucial environmental variables for waterbird population distribution patterns at the community, foraging guild and species levels were represented by the predictor importance index in the model output. Normality and one-way ANOVA tests and regression analysis were performed using IBM SPSS Statistics version 21.

3. Results

3.1. Crucial sites for waterbird population distributions

A total of 937,927 individuals, which correspond to 67 species, were recorded in the seven natural wetland in wintering seasons during 2003/2004–2016/2017. Twelve rare species (listed by IUCN, 2016, Appendix 51) were observed, of which 2 species (Siberian crane Grus leucogeranus, Baer’s pochard Aythya baeri) was listed as critically endangered, 1 species (Oriental White Stork Ciconia boyciana) was listed as endangered, 5 species were vulnerable (Lesser white-fronted goose Anser erythropus, Swan goose A. cygnoides, Hooded crane Grus monacha, White-naped crane Grus vipio, Common pochard Aythya ferina), 4 species were near-threatened (Falcated duck A. falcata, Ferruginous duck A. nyroca, Black-tailed godwit Limosa limosa, Eurasian curlew Numenius arquata).

At the community level, the species number was highest in Daxiaoxi lake, followed by Chunfeng, Baihu lakes and Dingzi dyke, but lowest in Tanjiaweizi, Junshanhou and Hongqi lakes (F6, 53 = 9.35, p < 0.001; Fig. 2a). The abundances in Daxiaoxi and Baihu lakes followed by Dingzi dyke were higher than those in other sites (F6, 53 = 7.90, p < 0.001; Fig. 2b). The densities in Daxiaoxi lake followed with Tanjiaweizi were higher than those in other sites (F6, 53 = 9.61, p < 0.001; Fig. 2c). The SHDI was lowest in Tanjiaweizi than those in other sites (F6, 53 = 3.69, p < 0.01; Fig. 2d).

At the foraging guild level, the seven natural wetlands were not utilized equally by the five guilds of waterbirds. (Fig. 3). Specifically, tuber feeders were found to prefer inhabiting in Baihu lake and Tanjiaweizi (F6, 53 = 2.54, p = 0.03 < 0.05; Fig. 3), whereas herbivores and omnivores especially prefer Daxiaoxi lake, with the density in this site significantly higher than that of others (herbivores, F6, 53 = 6.80, p < 0.01; omnivores, F6, 53 = 8.43, p < 0.001; Fig. 3). Higher densities of fish eaters and invertebrate eaters were found in Daxiaoxi and Dingzi dyke, and in Baihu lake for the latter foraging guild (fish eaters, F6, 53 = 4.69, p < 0.01; invertebrate eaters, F6, 53 = 3.53, p < 0.01; Fig. 3).

At the species level, each species exhibited unique and complex site preferences inferred by their different densities in the seven natural wetlands (Fig. 4). The densities of Common crane were higher in Dingzi dyke, Tanjiaweizi and Daxiaoxi lake than those in other sites (F6, 53 = 7.80, p < 0.001; Fig. 4). Tundra swans and Eurasian spoonbills exhibited similar site preferences as indicated by their highest densities in Baihu lake (Tundra swans, F6, 53 = 2.69, p < 0.05; Eurasian spoonbills, F6, 53 = 6.59, p < 0.001; Fig. 4). Bean geese and Lesser white-fronted geese also exhibited similar distribution patterns, with their significantly higher densities in Daxiaoxi lake than those in other sites (Bean geese, F6, 53 = 5.75, p < 0.01; Lesser white-fronted geese, F6, 53 = 5.22, p < 0.001; Fig. 4). Great cormorant was the most common in Daxiaoxi lake and Dingzi dyke as indicated by the significantly higher densities in these two sites (F6, 53 = 6.63, p < 0.001; Fig. 4). Different from other species, Grey herons distributed evenly in the seven natural wetlands, with no significant difference in densities (F6, 53 = 1.78, p = 0.12 > 0.05; Fig. 4). Dunlins had higher densities in Dingzi dyke and Baihu lake than those in other sites (F6, 53 = 2.62, p < 0.05; Fig. 4). Falcated ducks and Common teals exhibited similar distribution patterns as indicated by their highest densities in Daxiaoxi lake (Falcated ducks, F6, 53 = 6.90, p < 0.001; Common teals, F6, 53 = 3.94, p < 0.01; Fig. 4).

On the whole, among the seven selected natural wetlands, five natural wetlands, i.e., Daxiaoxi, Chunfeng, Baihu lakes, Dingzi dyke and
Tanjiaweizi, were the crucial sites for wintering migratory waterbird in East Dongting Lake, inferred by the higher waterbirds populations at the community, foraging guild and species levels in these wetlands (Figs. 2–4).

3.2. Environmental variables in seven natural wetlands

After accuracy assessment of the individual classifications (water, mudflat and vegetation habitats) with a standard error matrix (confusion matrix) (Dadaser-Celik et al., 2008), the overall accuracies of all classifications (2003/2004–2016/2017, using reference data from the GoogleEarth images) were >90%, whereas the kappa statistic values for the same classifications were >0.9. Ten environmental variables all exhibited significant differences in the seven natural wetlands (Fig. 5). Specifically, the mudflat areas were highest in Chunfeng lake and Dingzi dyke, followed by Daxiaoxi, Junshanhou, Baihu, and Hongqi lakes, but lowest in Tanjiaweizi ($F_{6, 53} = 2.59, p < 0.05$). The vegetation areas were highest in Chunfeng lake, followed by Dingzi dyke, moderate in Junshanhou and Hongqi lakes, but lowest in Daxiaoxi, Baihu lakes and Tanjiaweizi ($F_{6, 53} = 19.95, p < 0.001$). The shallow water areas with the depth of 0–50 cm exhibited similar site distribution, with the largest area in

Fig. 2. Waterbird species number (a), density (b), abundance (c) and diversity (SHDI, d) at the community level in the seven natural wetlands. DX: Daxiaoxi lake; CF: Chunfeng lake; DZ: Dingzi dyke; JS: Junshanhou lake; TJ: Tanjiaweizi; BH: Baihu lake; HQ: Hongqi lake. ** denotes $p < 0.01$; * denotes $p < 0.05$; # denotes $p < 0.1$.

Fig. 3. Densities of five waterbird guilds (Tuber feeders, Herbivores, Fish eater, Invertebrate eaters, Omnivores) in the seven natural wetlands. DX: Daxiaoxi lake; CF: Chunfeng lake; DZ: Dingzi dyke; JS: Junshanhou lake; TJ: Tanjiaweizi; BH: Baihu lake; HQ: Hongqi lake. ** denotes $p < 0.01$; * denotes $p < 0.05$; # denotes $p < 0.1$. 
Fig. 4. Densities of ten threatened or dominant species in the seven natural wetlands. DX: Daxiaoxi lake; CF: Chunfeng lake; DZ: Dingzi dyke; JS: Junshanhou lake; TJ: Tanjiaweizi; BH: Baihu lake; HQ: Hongqi lake. ** denotes p < 0.01; * denotes p < 0.05; # denotes p < 0.1.
Fig. 5. Environmental variables in the seven natural wetlands. DX: Daxiaoxi lake; CF: Chunfeng lake; DZ: Dingzi dyke; JS: Junshanhou lake; TJ: Tanjiaweizi; BH: Baihu lake; HQ: Hongqi lake.

** denotes p < 0.01; * denotes p < 0.05; # denotes p < 0.1.
Baihu lake (0–20 cm, F<sub>53</sub> = 4.59, p < 0.01; 20–50 cm, F<sub>53</sub> = 3.35, p < 0.05). The water areas with the depth of 50–100 cm were higher in Baihu, Chunfeng lakes and Dingzi dyke than those in other sites (F<sub>53</sub> = 2.83, p < 0.05). The water areas with the depth >100 cm were highest in Chunfeng lake and Dingzi dyke than those in other sites (F<sub>53</sub> = 5.51, p < 0.01). The mean and max NDVIs exhibited the similar distributions, which were higher in TANJIWEI, Junshanhou, Hongqi, Chunfeng lakes and Dingzi dyke, but lower in DAXIAOXI and Baihu lakes (mean NDVI, F<sub>53</sub> = 3.08, p < 0.05; max NDVI, F<sub>53</sub> = 2.88, p < 0.05). The min NDVI was highest in TANJIWEI, followed by Hongqi lake, than those in other sites (F<sub>53</sub> = 2.78, p < 0.05). According to our classification (Details were presented in the Methods section), human disturbance were the highest in Chunfeng, Junshanhou lakes and TANJIWEI (classified as ‘3’), the moderate in Hongqi lake and Dingzi dyke (classified as ‘2’), but the lowest in DAXIAOXI and Baihu lakes (classified as ‘1’).

3.3. Crucial environmental variables affecting waterbird population distributions

At the community level, the species number exhibited significant positive linear correlations with water area with the depth >100 cm (p < 0.01) and vegetation area (p < 0.05), but negative with disturbance (p < 0.01) and mudflat area (p < 0.05) (Tables 2 & 3), among which water area with the depth >100 cm and disturbance were the most two important environmental variables (Table 3). Waterbird density was positively correlated with water area with the depth >100 cm and vegetation area, and the former variable was more important (Table 3). The abundance was negatively correlated with disturbance but positively correlated with water area with the depth >100 cm (Table 3), while disturbance was the most important variable (Table 3). The species diversity (SHDI) was negatively correlated with the min NDVI and disturbance, while min NDVI was the most important variable (Table 3).

At the foraging guild level, the densities of the five foraging guilds, except herbivores, all exhibited significant correlations with the environmental variables that appeared to be foraging guild-specific (Tables 2 and 3). Specifically, the density of tuber feeder was positively correlated with min NDVI and water area with the depth of 50–100 cm, while min NDVI was the most important variable; the density of fish eaters was negatively correlated with disturbance and water area with the depths of 20–50 cm but positively with water area with the depth of 50–100 cm, while disturbance was the most important variable; the density of invertebrate eaters was positively correlated with water area with the depths of 20–50 cm; and the density of omnivores was positively correlated with water area with the depth >100 cm and vegetation area, while water area with the depth >100 cm was the most important variable.

At the species level, among 10 selected threatened or dominated species, the densities of 8 species were significantly correlated with the environmental variables that appeared to be species-specific (Tables 2 and 3). Specifically, Tundra swan density was positively correlated with water areas with the depths of 20–50 cm and 50–100 cm, while water area with the depth of 20–50 cm was the most important variable; the densities of Bean goose and Lesser white-fronted goose both exhibited Gaussian distributions with the mean NDVI of sedge meadows (Bean Goose, Amplitude = 5.976, Mean = 0.27, SD = 0.08; Lesser White-Fronted Goose, Amplitude = 3.219, Mean = 0.24, SD = 0.08; Table 2); Great cormorant density was positively correlated with water area with the depth >100 cm; Eurasian spoonbill density was positively correlated with water area with the depth of 20–50 cm and mudflat area but negatively with the water area with the depth of 50–100 cm, while water area with the depth of 20–50 cm was the most important variable; Dunlin density was positively correlated with water area with the depth of 0–20 cm; Falcated duck density was positively correlated with water area with the depth >100 cm but negatively with vegetation area, while water area with the depth >100 cm was the most important variable; Common teal density was positively correlated with water area with the depth >100 cm.

4. Discussion

In the context of large-scale hydraulic engineering (anthroposphere), it is of great concern worldwide to elucidate the possible impacts of hydrological regime (hydrosphere) on food availabilities and thereby the distribution pattern of wetland biodiversity (biosphere). The present study, which evaluated 10 wintering seasons during 2003/2004–2016/2017 in the East Dongting Lake, revealed that five natural wetlands, i.e., DAXIAOXI, Chunfeng, Baihu lakes, Dingzi dyke and TANJIWEI were the crucial wintering sites for migratory waterbird in the East Dongting Lake, inferred by the higher waterbirds populations at the community, foraging guild and species levels in these wetlands (Figs. 2–4).

**Table 2**

Results of forward stepwise linear regression and Gaussian regression of waterbird populations and environmental variables.

<table>
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<th>Levels</th>
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<th>Environmental variable</th>
<th>F</th>
<th>df</th>
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<td>0.08</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Lesser white-fronted goose&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Mean NDVI</td>
<td>3.49</td>
<td>0.23</td>
<td>0.08</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Great Cormorant</td>
<td>Water area (&gt;100 cm)</td>
<td>6.526</td>
<td>1.31</td>
<td>0.016</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Eurasian Spoonbill</td>
<td>Water area (20–50 cm), Water area (&gt;100 cm), Mudflat area</td>
<td>76.961</td>
<td>3.29</td>
<td>&lt;0.001</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Dunlin</td>
<td>Water area (0–20 cm)</td>
<td>4.346</td>
<td>1.31</td>
<td>0.045</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Falcated duck</td>
<td>Water area (&gt;100 cm), Vegetation area</td>
<td>31.877</td>
<td>2.30</td>
<td>&lt;0.001</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>Common teal</td>
<td>Water area (&gt;100 cm)</td>
<td>23.85</td>
<td>1.31</td>
<td>&lt;0.001</td>
<td>0.42</td>
</tr>
</tbody>
</table>

<sup>a</sup> The units is hectare (ha) for the area of water, vegetation and mudflat.

<sup>b</sup> Denotes the densities of waterbirds at the foraging guild and species levels. Water area (0–20 cm), water area (20–50 cm), water area (50–100 cm) and water area (>100 cm) represented the water areas with the depth of 0–20 cm, 20–50 cm, 50–100 cm and >100 cm, respectively.

<sup>c</sup> Gaussian regressions were used to analyze the correlations between the densities of Bean goose and Lesser white-fronted goose and environmental variables. The regression models were: Bean goose, \( y = 6.11 \times e^{−0.25(\bar{x}−0.28)²/0.08²}\); Lesser white-fronted goose, \( y = 3.49 \times e^{−0.55(\bar{x}−0.21)²/0.10²}\).

<sup>d</sup> p represents the significant different value.
Given the distinct feeding requirements of specific waterbird assemblages (Bellio et al., 2009), different feeding conditions might lead to different waterbird compositions and distributions among different sites, as indicated by the relationships between waterbird populations and environmental variables in present study (Tables 2–3). Waterbird population distributions exhibited strong responses to the environmental variables in East Dongting Lake (Tables 2–3), in particular the crucial environmental variables, including the water areas with the depths of 0–20 cm, 20–50 cm, and >100 cm, the growth status of vegetation (Mean and Min NDVI), and human disturbance (Table 3). Moreover, the crucial environmental variables differed among waterbirds at the community, foraging guild and species levels as indicated by the importance of environmental variables (Tables 3), which might lead to differences of the waterbird populations and distributions in the seven selected natural wetlands (Figs. 2–4). We inferred that sufficient available feeding habitats (Fig. 5) might be the most probable reason of the unique and complex distributions of waterbirds in the seven natural wetlands (Figs. 2–4).

Water depth is the most important factor limiting the habitat use of waterbirds (Isola et al., 2000; Ma et al., 2010). Shallow water habitats are more productive where prey concentrate (Kingsford and Porter, 1994). Water depth directly determines the accessibility of foraging habitats and the feeding success for waterbirds because of the restrictions of bird morphology, e.g. the lengths of legs, bills and necks (Collazo et al., 2002; Poyra, 1983). Many shorebird species, e.g. Dunlin in our study, preferred water area with the depth <20 cm (Isola et al., 2000) and fed almost exclusively on invertebrates (Thompson et al., 1992), as indicated by the significant positive correlations between the water area with the depth of 0–20 cm and the density of Dunlins (Tables 2–3). Larger species with longer bills, necks and legs can easily forage in deeper water habitats than smaller taxa (Ma et al., 2010). Zhang et al. (2014) recognized that Eurasian spoonbill preferred the foraging water habitats with the depth of 23.0 ± 5.6 cm. Previous studies illustrated that Tundra swan with longer necks could forage in water habitats with greater range of water depths from 0 to 70 cm (Nolet et al., 2002; Zhang et al., 2014). Our results indicated that the densities of Tundra swan and Eurasian spoonbill were significantly positively correlated with the water area with the depth of 20–50 cm in the seven natural wetlands (Tables 2–3). Dabbling ducks, e.g. Falcated duck and Common teal in our study, can swim and forage in deep water habitats with the depth >100 cm (Ma et al., 2010). Deep water habitat means various food resources which probably results in the higher density of omnivores ducks foraging in such habitats, as indicated by the strong positive correlations between the water area with the depth >100 cm and the densities of Falcated duck and Common teal in the present study (Tables 2–3). Consequently, water area with different depths might be the most probable causes leading to the populations and distributions of tuber feeders (e.g. Tundra swan), invertebrate eaters (e.g. Eurasian spoonbill and Dunlin) and omnivores (e.g. Falcated duck and Common teal) in the seven natural wetlands.

Vegetation in particular the sedge meadows are crucial foraging habitats for herbivores geese (Cong et al., 2012; X. Wang et al., 2013a; Zhao et al., 2010; Zhao et al., 2015) as well as omnivores. In the present study, the growth status of vegetation in particular the mean and min NDVI were crucial environmental variable for waterbirds (Tables 2–3). Beyond providing food resources such as leaves, tubers and rhizomes for herbivores (e.g. herbivores geese) and tuber feeders (e.g. crane), the increasing NDVI of vegetation means the higher food availability for herbivores (e.g. herbivores geese) and tuber feeders (e.g. crane), the increasing NDVI of vegetation means the higher food availability for herbivores thereby leading to the increase of herbivores populations, however, high and dense vegetation (e.g. too higher NDVI) can limit the accessibility of wetlands, thus adversely affect foraging and prey detection of herbivores (Fujitsuka et al., 2001). Therefore, too high NDVI can lead to decreased numbers of herbivores. This phenomenon was strongly illustrated by the Gaussian distribution of the densities of Bean goose and Lesser white-fronted goose along the mean NDVI in the seven natural wetlands (Tables 2–3). Tubers and rhizomes of short and sparse vegetation were the main food resources for tuber feeders, e.g. Common crane (Wu et al., 2014). This could explain the positive

### Table 3

The importance of the driving environmental factors affecting waterbird population distributions in East Dongting Lake.

<table>
<thead>
<tr>
<th>Levels</th>
<th>Species variable</th>
<th>Environmental variable</th>
<th>Coefficient</th>
<th>Importance</th>
<th>p*&lt;sup&gt;**&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community level</td>
<td>Species number</td>
<td>Water area (&gt;100 cm)</td>
<td>0.135</td>
<td>0.427</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Disurbance</td>
<td>-5.887</td>
<td>0.303</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vegetation area</td>
<td>0.006</td>
<td>0.162</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mudflat area</td>
<td>-0.008</td>
<td>0.108</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>Density</td>
<td>Water area (&gt;100 cm)</td>
<td>0.28</td>
<td>0.705</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vegetation area</td>
<td>0.006</td>
<td>0.295</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>Abundance</td>
<td>Disurbance</td>
<td>-9925.86</td>
<td>0.776</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Water area (&gt;100 cm)</td>
<td>231.189</td>
<td>0.224</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>SHDI</td>
<td>Min NDVI</td>
<td>-3.864</td>
<td>0.75</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Disurbance</td>
<td>-0.314</td>
<td>0.25</td>
<td>0.036</td>
</tr>
<tr>
<td>Foraging guild level</td>
<td>Tuber feeder</td>
<td>Water area (50–100 cm)</td>
<td>4.392</td>
<td>0.735</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fish eaters</td>
<td>-0.001</td>
<td>0.265</td>
<td>0.128</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Water area (20–50 cm)</td>
<td>-0.311</td>
<td>0.503</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Water area (50–100 cm)</td>
<td>0.002</td>
<td>0.146</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>Invertebrate eaters</td>
<td>Water area (20–50 cm)</td>
<td>0.001</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Omnivores</td>
<td>0.149</td>
<td>0.864</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vegetation area</td>
<td>0.002</td>
<td>0.136</td>
<td>0.01</td>
</tr>
<tr>
<td>Species level</td>
<td>Tundra Swan</td>
<td>Water area (20–50 cm)</td>
<td>0.001</td>
<td>0.648</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td>Great Cormorant</td>
<td>Water area (&gt;100 cm)</td>
<td>0.004</td>
<td>1</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Eurasian Spoonbill</td>
<td>Water area (20–50 cm)</td>
<td>0.01</td>
<td>0.883</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td></td>
<td>Water area (50–100 cm)</td>
<td>-0.001</td>
<td>0.082</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Dunlin</td>
<td>Water area (0–20 cm)</td>
<td>0.004</td>
<td>1</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td>Falcated duck</td>
<td>Water area (&gt;100 cm)</td>
<td>0.117</td>
<td>0.898</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vegetable area</td>
<td>-0.001</td>
<td>0.102</td>
<td>0.049</td>
</tr>
<tr>
<td></td>
<td>Common teal</td>
<td>Water area (&gt;100 cm)</td>
<td>0.03</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

*<sup>a</sup> The units is hectare (ha) for the area of water, vegetation and mudflat. Water area (0–20 cm), Water area (20–50 cm), water area (50–100 cm) and water area (>100 cm) represented the water areas with the depth of 0–20 cm, 20–50 cm, 50–100 cm and >100 cm, respectively.

*<sup>b</sup> Denotes the densities of waterbirds at the foraging guild and species levels.

*<sup>**</sup> p represents the significant different value.
correlation between the density of tuber feeders and the min NDVI in the natural wetlands (Tables 2–3). Consequently, the growth status of vegetation might be probable causes that effect the populations and distributions of herbivores (e.g. Bean goose and Lesser white-fronted goose) and tuber feeders (e.g. crane).

Foraging animals must cope with the potential risk, e.g. human disturbance (Jonker et al., 2010). It was reported by Yuan et al. (2014) that human disturbance was recognized as a crucial environmental variable affecting the populations and distributions of waterbirds. Waterbirds were more distant from roads (though with no higher traffic) and human settlements, therefore sites with less disturbance or the early detection of approaching disturbance should therefore be preferred (Rosin et al., 2012). In the present study, significant negative correlations were observed between human disturbance and the species number, abundance and species diversity (SHDI) at the community level and the density of fish eaters (Tables 2–3). The negative correlation between human disturbance and populations and distributions of waterbirds may be linked with two reasons in our study area. Closer to roads might represent higher predation risk, e.g. lower waterbird populations in Junshanhou lake (Figs. 2–4). What's more, fish and reed harvesting occurred throughout the East Dongting Lake, except at Daxiaoxi lake (where there is closed management) in wintering seasons, which might be also the potential risk.

Other variables, which were not analyzed in this study, may also influence the populations and distributions of wintering waterbirds. More importantly, previous studies suggested that the water recession time were adversely correlated with the wintering waterbird populations in East Dongting Lake (Guan et al., 2014; Zou et al., 2017). Water recession time might first influence the food availability and thereby the waterbird populations and distributions (Zhao et al., 2012). Therefore, water recession time was the important consideration when evaluating wintering waterbird community patterns in future studies.

4.1. Conservation implications

According to our results, the following conservation measures were suggested to be quickly implemented. Firstly, it is important to strengthen the protection and management of Daxiaoxi, Chunfeng, Baihu lakes, Dingzi dyke and Tanjiaweizi, since these five wetlands were crucial sites for wintering migratory waterbirds in East Dongting Lake. Secondly, according to the three crucial environmental variables for waterbirds, i.e., water area with the depths of 0–20 cm, 20–50 cm and >100 cm, regionally water level regulations were necessary to maintained large water areas with suitable water depths. Thirdly, water recession should not occur too early (before September, Zou et al., 2017) or too late (after November, Guan et al., 2014), so that complete sedge Carex meadow vegetation exposure could be ensured and thus maintaining large areas of moderate growth status (Mean NDVI) of vegetation. Lastly, the harmful human disturbance must be avoided in five valuable sites and the closed management of particularly sensitive habitats should be considered, such as the closed management in Daxiaoxi lake.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.11.185.

References


Acknowledgements

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