**Dyke demolition led to a sharp decline in waterbird diversity due to reduction in habitat quality: A case study of Dongting Lake, China**

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**Abstract:**

Waterbird responses to habitat changes are of great concern in ecology. Dongting Lake is the second-largest freshwater lake in China, and its vast wetland area provides an important wintering habitat for migratory waterbirds of the East Asian–Australasian Flyway. However, lake reclamation and illegal human-made dykes have degraded the Dongting Lake wetland area at different degrees in the recent decades, seriously threatening the ecology of this area. In 2017, to restore the natural properties of Dongting Lake, the Chinese government completely demolished 459 dykes and preserved 14 dykes for various purposes (biodiversity conservation and flood control). However, the direct impact of dyke demolition on wintering waterbirds has not been comprehensively assessed. In this study, based on annual (2013/14–2020/21) waterbird census data, we compared the differences in species composition of waterbirds in the dyke-demolished and dyke-preserved areas. The results indicated that waterbird diversity, in terms of species number, abundance, the proportion of abundance, number of rare waterbirds species, and exclusive species, was higher in the dyke preserved areas than in the previously demolished areas. Species turnover and reordering further identified dynamic differences in the spatial and temporal distributions of waterbirds. Therefore, we used long-term habitat data to explore whether habitat changes were responsible for the changes in waterbirds; the results showed significantly decreased water and mudflat areas, but a significantly increased vegetation area in the dyke-demolished areas. The water area was significantly positively correlated with waterbirds in this habitat. Compared to the dyke-demolished areas, the stable and suitable habitat area in the dyke-preserved areas might be closely related to the higher waterbird diversity. Our study revealed habitat changes in the context of large-scale dyke demolition in Dongting Lake and demonstrated the dynamic response of waterbirds to habitat changes.

**Keywords:** biodiversity, waterbird, wetlands, Dyke demolition, habitat change, Dongting Lake

**1. Introduction**

Diversity and vulnerability are fundamental characteristics of wetland ecosystems, which are closely linked by several factors. Although wetlands can maintain high biodiversity (Hansson et al. 2005, Zedler and Kercher 2005), they are vulnerable to various stressors and are globally threatened, especially by human activities (Hu et al. 2017, Dang et al. 2020). In general, human activity alters the hydrological regimes of wetlands and thus poses a threat to their biodiversity (Foti et al. 2013, Palmer and Ruhi 2019, Jones et al. 2021). Therefore, the impact of anthropogenic modifications of wetland hydrological regimes on biodiversity has important research implications.

The Yangtze River floodplain is subject to monsoonal flooding and seasonal hydrological fluctuations (inundation and reduction of water levels in summer and autumn, respectively) (Fang et al. 2006, Liu et al. 2020). This unique hydrological cycle creates many extensive and ephemeral artificial and natural wetlands (Xia et al. 2017), which support more than one million wintering waterbirds along the East Asian-Australasian Flyway, including populations of several globally threatened species (Cao et al. 2010, Wang et al. 2017). Unfortunately, in the past half-century, the area of wetlands has severely degraded in the middle reaches of the Yangtze River basin (Cui et al. 2013). Xie et al. (2017) recently reported that from 1975 to 2015, 2132.3 ± 219.6 km2 of area was lost from the total area of all lakes in the middle and lower reaches of the Yangtze River, with Dongting Lake experiencing the most obvious decline (855.1 ± 131.8 km2). Similarly, the health of wetland ecosystems is also declining (Sun et al. 2017). Human activities and excessive reclamation are the main driving factors leading to wetland degradation (Du et al. 2011, Hou et al. 2020b). Although the area of wetlands in the middle and lower reaches of the Yangtze River basin has gradually decreased in recent years, it is still the crucial wintering habitat for migratory waterbirds in China. Waterbird communities are key indicators for assessing wetland health and ecosystem services, because they respond to variations in wetland environmental factors (Kingsford 1999, Williamson et al. 2013, Ogden et al. 2014). Therefore, environmental shifts in wetland ecosystems can be visually reflected by waterbird diversity.

Dongting Lake, located in the middle and lower reaches of the Yangtze River, is the second-largest freshwater lake in China and one of the 200 priority ecoregions for global conservation (Olson and Dinerstein 2002). The Yangtze River Plain has been intensively exploited with the development of the social economy by human activities such as the construction of the Three Gorges Dam, reclamation, and sand mining. After the operation of the Three Gorges Dam, the inundation duration of the lake wetland inevitably changed, disrupting the habitat suitability for wintering waterbirds in Dongting Lake (Sun et al. 2012, Wu et al. 2020). Earthen dykes were historically constructed in the Dongting Lake area as part of lake reclamation activities and belonged to three main categories: illegal dykes constructed by fishermen for fishing, dykes constructed for the centralized elimination of *Oncomelania hupensis hupensis* snails (intermediate hosts of *Schistosoma japonicum*) (Li et al. 2000), and ecological dykes constructed for the protection of waterbirds (Zou et al. 2019). Lake reclamation has produced a series of serious and far-reaching environmental impacts, such as reduced hydrological connectivity (Nakayama and Watanabe 2008), sedimentation (Xu et al. 2017), and biodiversity reduction (Fang et al. 2006). Therefore, adhering to the concept of sustainable development, the Chinese government proposed "to step up conservation of the Yangtze River and stop its over development" for the Yangtze River Economic Belt (Xiang et al. 2021). To repair the ecological damage of Dongting Lake caused by lake reclamation, the Chinese government completely demolished 459 illegal dykes before the end of 2017 and preserved 14 ecological dykes for biodiversity protection and flood control. It has not been evaluated whether the massive demolition of the dykes has improved the ecological services of the wetlands and ultimately led to a significant increase in biodiversity, as expected by government agencies.

The impacts of dykes on wetland ecosystems are primarily related to habitat management, with dyked wetlands providing abundant food resources to maintain high waterbird diversity by regulating water levels (Murkin et al. 1982, Wang et al. 2020). Although the dykes in Dongting Lake were demolished on the basis that “dykes have negative effects on waterbird diversity”, studies have demonstrated that "ecological dykes have positive effects on maintaining waterbird diversity", which seems to be contradictory. Certainly, the government has preserved 14 ecological dykes, which fully illustrates the positive effect of ecological dykes. However, of the 459 dykes in Dongting Lake that were abruptly and ubiquitously demolished, several ecological dykes with important waterbird diversity conservation functions may have been “mistakenly demolished”. This could have a significant impact on wetland habitats and waterbird communities. Therefore, it is urgently required to comprehensively evaluate the effects of demolition of dykes (especially those that have proven to be ecologically important) on waterbird diversity.

A slow change in the ecosystem's external conditions can reduce its resilience without significantly affecting the equilibrium state (Scheffer and Carpenter 2003), and the ecosystem may appear stable. However, a sudden shift to a completely opposite regime can degrade this stability (Scheffer et al. 2001). As environmental drivers approach the critical point of ecological thresholds, communities change abruptly, with a series of species becoming extinct immediately and some gradually disappearing (Bestelmeyer et al. 2011, Dakos and Bascompte 2014). Several aspects of waterbird communities vary with space and time, especially when subjected to external environmental pressures; thus, a large number of diversity indicators are needed to quantify these variables. Species richness and number, species proportions, and foraging guild classification are commonly used metrics for analyzing the diversity of waterbirds in different habitats (Zhang et al. 2018, Zou et al. 2019, Fan et al. 2021, Zhang et al. 2021b). Richness alone may obscure the internal dynamics of species composition, but species turnover provides further insight into the rate at which species disappear and appear over time (Poysa et al. 2019). Species reordering, which represents the ranking changes in the relative abundance of species in a community over time, is a less well-documented but important indicator that can be used to describe the response of communities to chronic environmental drivers (Hallett et al. 2016). All these indices are useful measures to quantify the response of waterbird communities to habitat destruction. Therefore, it is highly desirable to evaluate the response of waterbirds to abrupt habitat changes based on indicators such as species richness, abundance, species composition, species turnover, and species reordering.

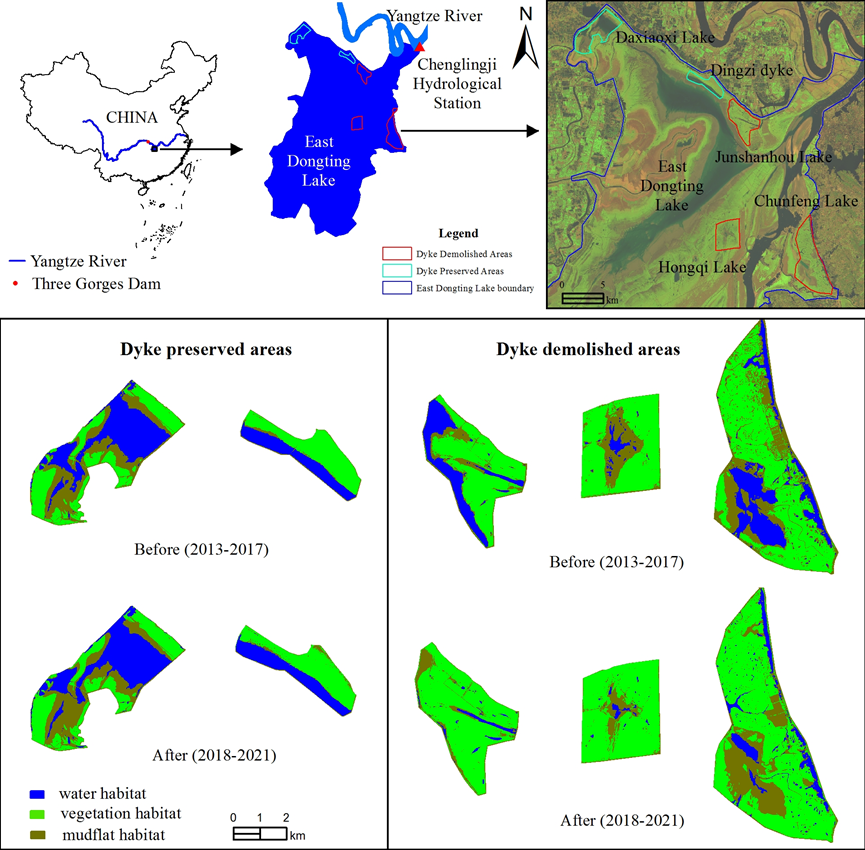
In summary, waterbird diversity due to dyke demolition in the Dongting Lake wetlands has not been comprehensively assessed. Using the East Dongting Lake wetland as an example, this study aims to: (1) reveal the effects of dyke demolition on habitat factors by comparing the differences in habitat factors in the dyke-demolished and dyke-preserved areas; (2) assess the changes in waterbird diversity due to dyke demolition based on the before-after monitoring data; and (3) explain the key mechanisms of dyke demolition on waterbird diversity by identifying the crucial factors for the waterbird’s differential use of the dyke-demolished and -preserved areas. The results would provide theoretical references for future wetland restoration in Dongting Lake, as well as suggestions for priority areas for waterbird diversity conservation.

**2. Materials and methods**

**2.1 Study area**

Dongting Lake is divided into eastern, southern, and western parts, and East Dongting Lake has been designated as a wetland of international importance by the Ramsar Convention (Nan et al. 2020). The lake landscape has undergone drastic changes due to seasonal and interannual water level fluctuations (Xie et al. 2015). Hydrological changes affect the growth rate of *Carex*, the main food source for herbivorous geese (Zhao et al. 2012, Guan et al. 2014). Due to the periodic inundation pattern of Dongting Lake, *Carex* spp. (Chen et al. 2011) usually have two growing seasons. Typically, the first growing season shows rapid vegetative growth after flooding (usually between mid to late October and December); the aboveground plant parts gradually wither in January as the temperature decreases. Subsequently, *Carex* germinates again during the second growing season and continues to grow until flooding (Deng et al. 2013).

The East Dongting Lake National Nature Reserve (EDLNNR) (112°43′–113°14′ E, 29°0′–29°38′ N) is a Ramsar wetland with a total area of approximately 1900 km2. After years of monitoring, the Administrative Bureau of the EDLNNR has divided the core area and several important wintering habitats to facilitate regular waterbird surveys and conservation efforts. In this study, we selected Daxiaoxi Lake, Dingzi Dyke, Junshanhou Lake, Hongqi Lake, and Chunfeng Lake as the study areas (Fig. 1). According to the dyke demolition scheme and approved consent, the dykes along Daxiaoxi Lake and Dingzi Dyke within the core area were preserved, while the dykes along the other three areas were all demolished by the Chinese government in 2017.

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**Fig. 1** Study area and habitat changes before and after dyke demolition.

**2.2 Bird survey and analysis**

Wintering waterbirds were surveyed in the five selected natural wetlands from 2012/2013 to 2020/2021. Waterbird survey data were obtained from the Administrative Bureau of East Dongting Lake. With the assistance of the Administrative Bureau of East Dongting Lake Nature Reserve, comprehensive surveys of wintering waterbirds were simultaneously conducted according to the same protocol in the entire study area in mid-January every year, when the peak population of waterbirds was present. Following the same protocols (8–11 a.m. and 2–5 p.m., lasting three days), waterbirds were simultaneously investigated in the five study areas (Fig. 1) under sunny weather conditions. Two to three investigators, using 10 × 42 binoculars and 20× to 60× spotting scopes, observed and recorded the number of species and individuals of wintering waterbirds using the absolute number counting method.

Factors such as the breeding success of migratory birds and food availability at stopover sites can affect the population of migratory waterbirds (Baker et al. 2004, Tidwell et al. 2013). Therefore, it is inevitable that the population numbers and distribution of birds that migrate to their wintering areas (during the non-breeding phase) each year can be influenced. In this study, the percentage of wintering waterbird populations was used to replace the raw value of abundance to eliminate the inter-annual fluctuation of wintering waterbird population migration to the five study areas. More specifically, the proportion of abundance (%) of a species corresponds to the ratio of the number of individuals of the species in each area to the total number of individuals of the species in the five study areas.

To compare the impact of dyke demolition on waterbird diversity, we calculated species richness, abundance, and the proportion of waterbirds and assessed the differences in community composition between the dyke-demolished and -preserved areas before and after demolition. The wintering waterbird species were aggregated into five foraging guilds; tuber feeders, omnivores, insectivores, herbivores, and fish eaters based on their distinct feeding habits (Wu et al. 2014, Zhang et al. 2016, Zou et al. 2019). All the observed wintering waterbird species are listed in Appendix S1.

The East Dongting Lake wetlands are the major wintering habitats for waterbirds, especially threatened species. Threatened (listed as critically endangered, endangered, vulnerable, and near threatened on the IUCN Red List; IUCN, 2021), as well as common (species that appear in both areas) and exclusive (species that only appear in a single area) species were counted in dyke-demolished and -preserved areas. Tracking the population changes of dominant or threatened species and their relationship with the corresponding habitat can further determine the response of waterbirds to habitat changes. Twenty-three species of dominant or threatened waterbirds with large populations were selected to determine the correlation between waterbirds and the environment at the species level (Appendix S1).

**2.3. Habitat variables**

Habitat variables, including water area, mudflat area, vegetation area (sedge [*Carex* spp.] meadow area), and the normalized difference vegetation index (NDVI) of the vegetation were extracted from satellite images from 2013 to 2021 (Appendix S6). A total of 68 Landsat 5/8 or Sentinel-2 satellite images obtained from 2013 to 2021 were used to evaluate the changes in the areas of three habitats along water level gradients in the dyke-preserved areas as well as in the dyke-demolished areas before (2013–2017) and after the demolition of the dyke (2018–2021). Images acquired from mid-winter (January–February, with a similar period of waterbird surveys) from 2013 to 2021 were used to evaluate the impact of habitat changes on waterbird populations (Appendix S6). According to Zou et al. (2019), different habitat (vegetation, mudflat, and water) areas were extracted by the decision tree classification method with the help of the NDVI and the modified normalized difference water index (MNDWI), followed by classification accuracy evaluation for each image using a standard error matrix (confusion matrix) (Dadaser-Celik et al. 2008). Limited by the insufficient Landsat 5/8 images in the early overwintering period (November) and mid-overwintering period (January, similar to the period of waterbird surveys), the NDVI of vegetation that represents the food availability of geese was calculated from the MOD09Q1 dataset at a spatial resolution of 250 m and eight-day intervals (Terra MODIS images provided by the Earth Resources Observation Systems (EROS) data center, the United States Geological Survey (USGS)).

**2.4 Statistical analysis**

To further quantify the temporal variability of species composition in dyke-demolished and -preserved areas, we calculated and plotted turnover and mean rank shift over time. The calculation of turnover is based on the original formula of MacArthur and Wilson (1963). Diamond (1969) modified it to express proportional turnover to compare changes in bird richness over different years on the same island. The R package (codyn) developed by Hallett et al. (2016) calculates the species turnover between the two time periods, that is, the proportion of species gained and lost observed at both time points. We calculated the proportions of species appearance and disappearance in the dyke-demolished and -preserved areas from 2013 to 2021, respectively, while appearance and disappearance represented species gained and lost during that time interval.

The mean rank shift (MRS) is an indicator of the degree of species reordering between two-time points in a community (Collins et al. 2008). A higher MRS value indicates more reordering of the waterbird species. MRS is defined as:

where n is the species richness observed at both time points, t is the sample census year, and Ri,t is the relative rank of species i at time t.

Species turnover and MRS were performed using presence–absence data, and all statistical calculations were performed using the R package codyn(Hallett et al. 2016).

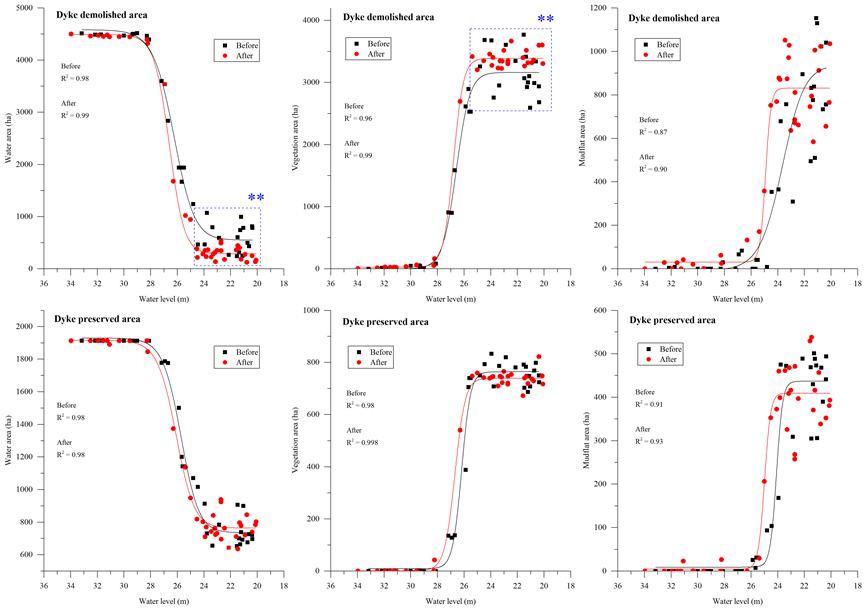
All data were assessed for normality using the Kolmogorov–Smirnov test. An independent sample t-test was used for normally distributed data, whereas the Mann–Whitney U test was used for non-normally distributed data. In all the statistical results, statistical significance was set at p < 0.05. Kolmogorov–Smirnov test and independent sample t-test and Mann–Whitney U test were performed using IBM SPSS Statistics version 23.0.

**3. Results**

**3.1 Habitat changes before and after dyke demolition**

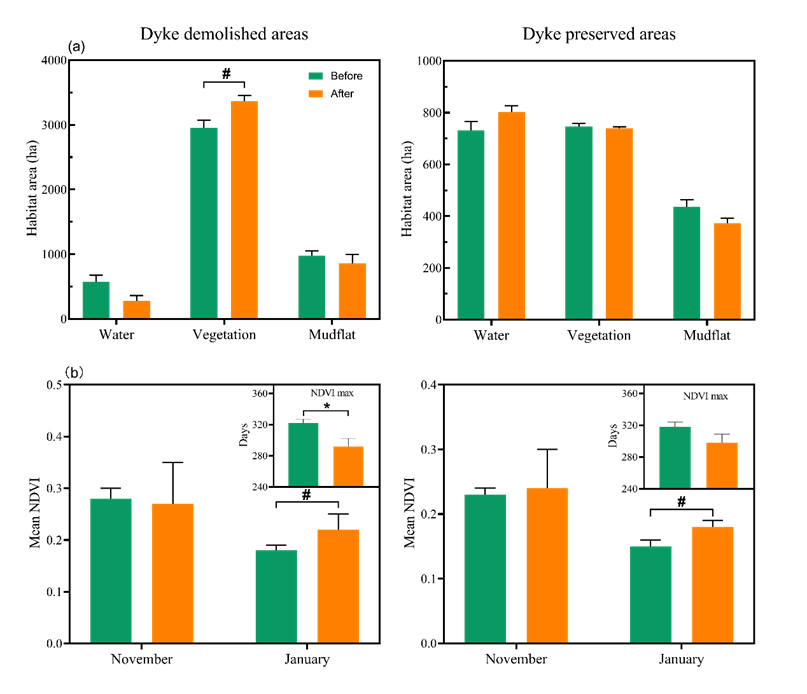
After accuracy assessment of the individual classifications (water, mudflat, and vegetation habitats) using a standard error matrix (confusion matrix) (Dadaser-Celik et al. 2008), the overall accuracies of all classifications (2011–2021, using reference data from the images) were >93%, while the kappa statistic values for the same classifications were >0.91.

The three types of habitats showed different changes in the dyke-demolished areas after demolition, with a significant increase in the area of vegetation habitat, but significant declines in the areas of water and mudflat habitats (Fig. 2). In contrast, no significant changes were observed in the three types of habitats in the dyke-preserved areas during the study period (Fig. 2).

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**Fig. 2** Changes in the areas of three habitats along the water level gradients in the dyke-preserved areas and dyke-demolished areas before (2013–2017) and after dyke demolition (2018–2021). The black dots and lines represent the average habitat area from 2013 to 2017 (before dyke demolition), and the red dots and lines represent the average habitat area from 2018 to 2021 (after dyke demolition). The water level is the current day's Chenglingji water level corresponding to the satellite image. \*\* denotes P < 0.01.

The three habitat variables in the dyke-demolished areas in January also exhibited before-and-after differences, with a significantly increased area of vegetation, a nearly half decreased water area, and a small decreased mudflat area (Fig. 3a). The dyke-preserved areas effectively have been maintaining a large water area over the long-term - providing valuable habitat to waterbirds that depend on it - and there is also little difference in vegetation and mudflat area (Fig. 3a). The NDVI in November exhibited similar distributions in both areas, however, the NDVI in January exhibited before and after differences, after which both were significantly higher than before (Fig. 3b). Meanwhile, the days of maximum NDVI in the dyke-demolished areas appeared significantly earlier, 30 days earlier (Fig. 3b).

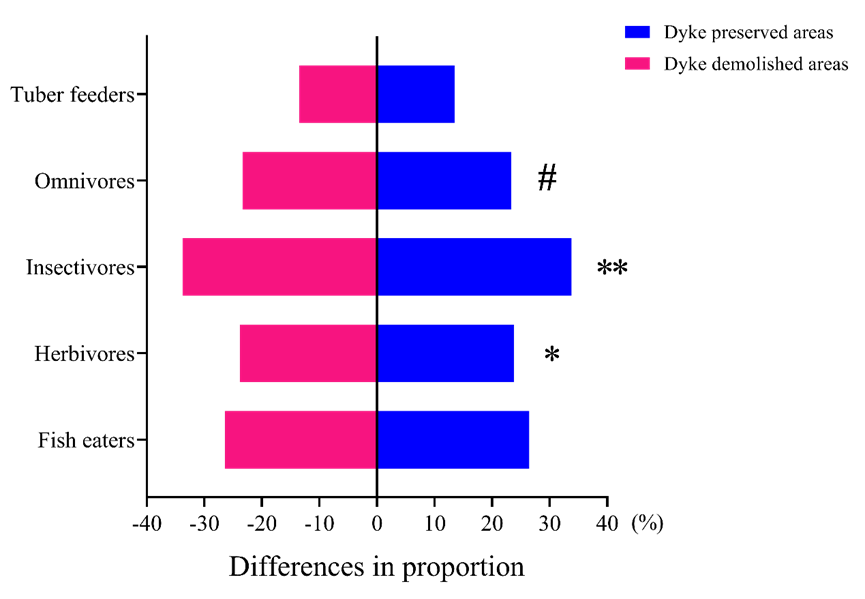
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**Fig. 3** Comparison of changes in (a) habitat area and (b) NDVI before and after dyke demolition. NDVImax represents the number of days when the vegetation reaches its maximum value in the first growing season. Error bars indicate the standard error of the mean. \* denotes p < 0.05; # denotes p < 0.1.

**3.2 Changes in species composition of waterbird communities**

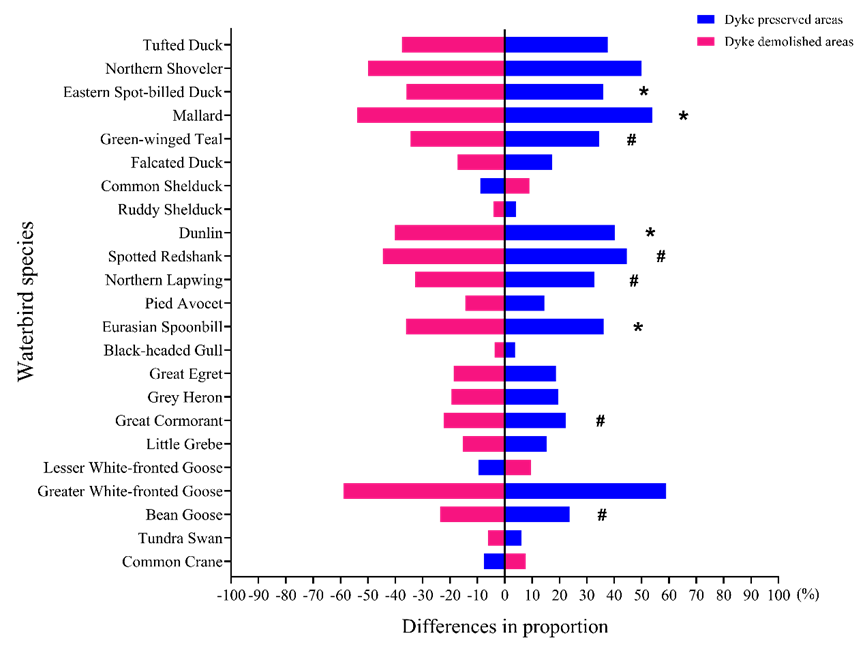
A total of 45,2021 individuals, corresponding to 62 species, were recorded in the entire study area during the winter seasons of 2012/2013–2020/2021 (Appendix S1). Among these, 50 species (126,100 individuals) were recorded in the dyke-demolished areas, accounting for 27.9 %, and nine rare species were observed (Appendix S1), while 55 species (325921 individuals) were recorded in dyke-preserved areas, accounting for 72.1 %, and 14 rare species were observed (Appendix S1). Before the dyke was demolished (2012/2013–2016/2017), the four matrices in dyke-demolished areas and dyke-preserved areas were: species number (48, 44), abundance (102930, 152751), proportion of abundance (40.3 %, 59.7 %), and number of rare waterbird species (8, 11), respectively. After the dyke was demolished (2017/2018-2020/2021), the four matrices in dyke-demolished areas and dyke-preserved areas were: species number (28, 48), abundance (23170, 173170), proportion of abundance (11.8 %, 88.2 %), and number of rare waterbird species (5, 10), respectively.

At the foraging guild level, there were obvious differences in distribution between the five guilds of waterbirds in the dyke-demolished areas and the preserved areas. In the two phases (2013–2017, 2018–2021) before and after the dyke was demolished, fish eaters, herbivores, insectivores, omnivores, and tuber feeders decreased by 26.44 %, 23.79 %, 33.8 %, 23.33 %, and 13.49 % respectively, in the dyke-demolished areas. In particular, the declining trends of insectivores, herbivores, and omnivores guilds reached significant levels of 0.01, 0.05, and 0.1, respectively (Fig. 4). The proportion of individuals that increased in the dyke preserved areas corresponded to a decrease in the proportion of dyke-demolished areas (Fig. 4).

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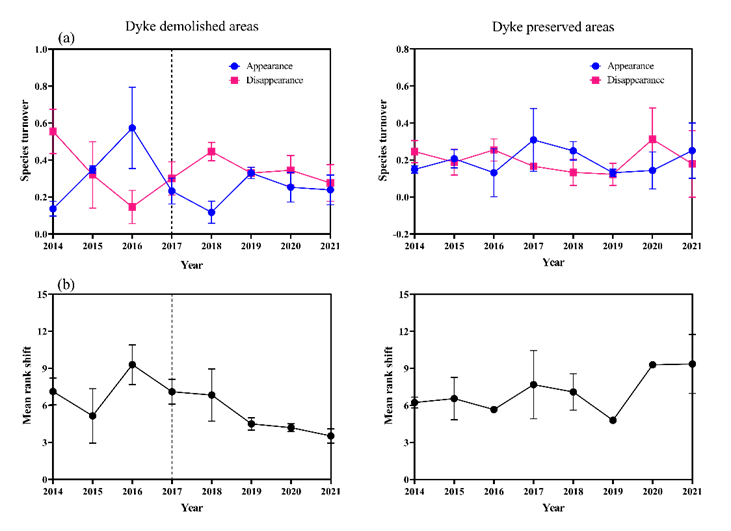
**Fig. 4** The difference in the proportion of five waterbird guilds between the dyke-demolished areas and the preserved areas in two phases, 2013–2017 and 2018–2021. \*\* denotes p < 0.01; \* denotes p < 0.05; **#** denotes p < 0.1.

At the species level, the habitat transfer of species before and after the dyke is demolished can be inferred from the difference in proportions between the dyke-demolished areas and the preserved areas (Fig. 5). After the dyke was demolished, almost all waterbird species showed different degrees of decline in the dyke-demolished areas, except for common crane, lesser white-fronted goose, and common shelduck, which had smaller increases (Fig. 5). On the contrary, most waterbird species were transferred to the dyke preserved areas, and their population capacity further increased (Fig. 5). Similarly, the exclusive species in the dyke preserved areas was higher than the demolished areas after the dyke was demolished, while the common species of the two types of habitats were significantly reduced. (Appendix S2).

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**Fig. 5** The difference in the proportion of species levels between the dyke-demolished areas and the preserved areas in the two phases of 2013-2017 and 2018-2021. \* denotes p < 0.05; **#** denotes p < 0.1.

Species composition in both dyke-demolished and preserved areas changed in stages after dyke demolition events. Species turnover changed drastically before 2018 in the dyke-demolished areas, but afterward, it was relatively smooth and the species disappearance rate was higher than the species appearance rate (Fig. 6). However, the species turnover in the dyke preserved areas remained stable for a long time, with small changes (Fig. 6). Furthermore, the mean rank shift of the dyke-demolished areas has continued to decline after 2017 but has increased in the dyke preserved areas (Fig. 6).

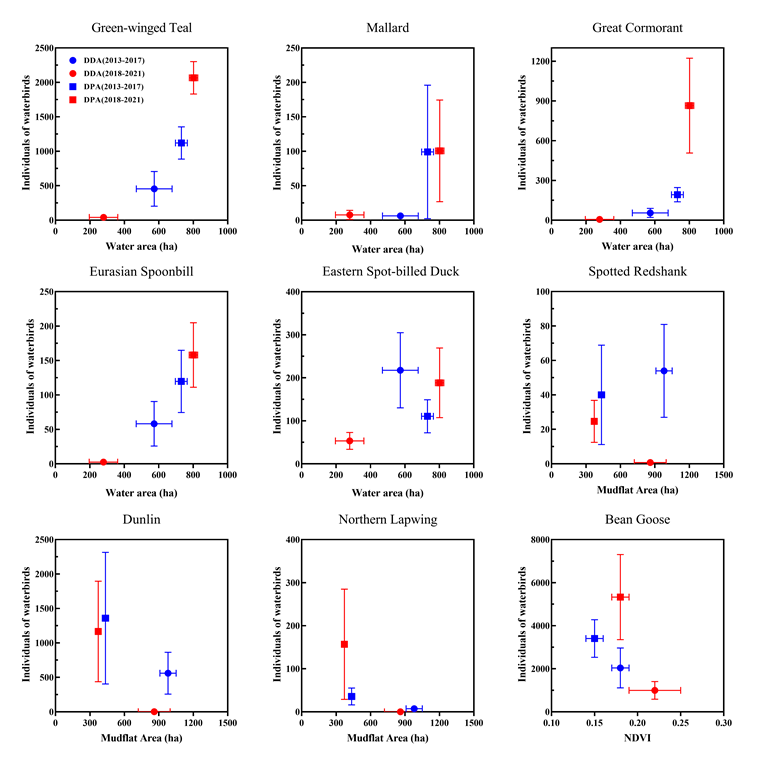
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**Fig. 6** Changes in species composition over time in two types of habitats. (a) Mean species turnover rate: turnover describes the cumulative year-to-year appearance and disappearance of all species. (b) Mean Rank shifts reveal the degree to which species reorder. The dotted line indicates the year when the dyke was demolished. Error bars represent standard error (SE).

**3.3 Relevant habitat variables causing differences in waterbird population distribution**

The foraging preferences of waterbirds can vary greatly among species, even among those that belong to the same foraging guild (Ma et al. 2010). The lesser white-fronted goose *Anser erythropus* is a globally threatened species, with over 90 percent overwintering in East Dongting Lake (Wang et al. 2012, Wang et al. 2013). Therefore, this study focused on nine species of waterbirds with significant variation, as well as lesser white-fronted geese, to evaluate the crucial habitat variables affecting the distribution of waterbirds. The habitat area on which waterbirds depend affects their abundance and distribution (Appendix S4, Fig. 7). Linear regression analysis showed that the green-winged teal (R2 =0.42, P=0.01), great cormorant (R2 =0.28, P=0.05), and Eurasian spoonbill (R2 =0.28, P=0.05) were positively correlated with the water area (Appendix S4). However, there was no significant correlation between the mallard (R2 =0.08, P=0.32) and eastern spot-billed duck (R2 =0.04, P=0.52) and water area (Appendix S4). No significant correlation was observed between spotted redshank (R2 =0.0008, P=0.92), Dunlin (R2 =0.17, P=0.14), northern lapwing (R2 =0.21, P=0.1), and mudflat areas (Appendix S4). Meanwhile, the bean goose and lesser white-fronted goose were not significantly correlated with NDVI (Appendix S3, S4), but bean goose were negatively correlated with vegetation area, and lesser white-fronted goose were not correlated with vegetation area (Appendix S5).

The abundance of Green-winged Teal, Mallard, Great Cormorant, Eurasian Spoonbill, and Eastern Spot-billed Duck, which depend on water bodies for foraging, decreased as the water area in the dyke-demolished areas decreased; however, their abundance increased in the dyke-preserved areas (Fig. 7). Similarly, for the spotted redshank, Dunlin, and northern lapwing, which depend on mudflats for foraging, their abundance plummeted to almost zero as the mudflat area in the dyke-demolished areas decreased; however, the abundance of northern lapwing increased in the preserved dyke areas, and Spotted Redshank and Dunlin were both relatively stable (Fig. 7). The abundance of bean geese decreased as NDVI values increased in the dyke-demolished areas, while the abundance of bean geese increased in the preserved dyke areas (Fig. 7).

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**Fig. 7** Relationship between the number of individuals of nine waterbird species with significant variation and their suitable habitat variables. DDA indicates dyke-demolished areas, DPA indicates dyke-preserved areas. Error bars represent standard errors (SE).

**4. Discussion**

Based on long-term monitoring data of waterbirds, this study investigated the spatiotemporal distribution dynamics of waterbirds due to changes in habitat hydrology and food availability caused by dyke demolition. We found that the demolition of the dyke during the receding water process resulted in significantly reduced wetland water area, reduced mudflat area, significantly increased vegetation area, and significantly earlier germination and growth of *Carex* spp. vegetation. In contrast, the dyked wetlands were able to maintain a stable area for the three habitat types. We also observed strong differences in the spatial and temporal distribution dynamics of waterbirds, which may be due to the sudden disruption of the long-standing and relatively stable "hydrology-habitat-waterbird diversity" balance in the East Dongting Lake caused by the demolition of the dyke. The key mechanisms affecting waterbird populations and distributions may vary by foraging guilds, habitat quality, and species.

For foraging guilds that are highly dependent on water, the mechanism of impact is a decrease in habitat availability. Suitable habitats for this foraging guild are generally water bodies, while water depth requirements generally vary according to feeding habits. For example, insectivores use shallow water as a foraging habitat (Safran et al. 1997), and omnivores and fish eaters use deep water as a foraging habitat (Paszkowski and Tonn 2006, Afdhal et al. 2013). In this study, we found that after the dykes were demolished in the wetland, a significant decrease in the area of suitable habitat for the highly water-dependent foraging guild occurred (Fig. 2), resulting in a significant reduction in the number of waterbirds in the guild (Fig. 4). Therefore, we speculate that the dyked wetland functioned well as a "water retainer" during the low-water period (wintering period for migratory birds), but after the dykes were demolished, their function was lost, resulting in a significantly decreased water area and eventually reduced numbers and changed the distribution of waterbirds that depend on this habitat. Related studies have also demonstrated that dyked wetlands have larger and deeper water areas than undyked wetlands (Monfils et al. 2014), providing suitable habitats for waterbirds that feed at different water depths (Weber and Haig 1996, Zhang et al. 2021b). Consequently, the stable water area and different water depth environments in the preserved dyke areas after the demolition of the dyke in other wetlands may be responsible for the increased proportion of insectivores, omnivores, and fish-eaters waterbirds (Fig. 4-5).

Compared to the significant changes in other foraging guilds before and after the demolition of the dyke, relatively small and extremely few species of tuber feeder waterbirds changed (only common crane and tundra swan). This was probably due to the relatively small species and the number of tuber feeder waterbirds in this study area (a total of six species with 5634 individuals were observed; of these, five species with 659 individuals were accounted for in the dyke-demolished areas) and were not the dominant species in the East Dongting Lake, however, we still analyzed the impact of the demolition of the dyke on these species due to them being endangered. The dominant food items of the cranes include *Polygonum criopolitanum* and *Potentilla limprichtii* which grow in the bottomlands, whose above-ground biomass varies significantly along the water level gradient (Zhang et al. 2013, Hou et al. 2021). The dominant food items of the tundra swan are submerged vegetation such as *Potamogeton crispus* and *Vallisneria natans* (Cong et al. 2011, Fox et al. 2011). Therefore, we speculate that the accelerated receding water caused by the demolition of the wetland dyke may lead to a longer growth time for the dominant food of cranes growing in the mudflats and bottomlands area, which may result in better food quality and ultimately an increased number of cranes in the dyke-demolished areas (Fig. 5). In addition, the decreased water area in the dyke-demolished areas may have caused a more rapid die-off of the previously less distributed submerged vegetation, and consequently reduced the number of tundra swans that feed on it (Fig. 4-5). Our results are similar to those related to the main wintering site (Poyang Lake) of cranes and tundra swan, where water level affects food availability and population abundance (Cong et al. 2011, Chen et al. 2016, Hou et al. 2020a).

The inter-annual variation in hydrological regimes (especially the timing of receding water) in Dongting Lake, influenced by the Three Gorges Dam and climate change, led to a high correlation between herbivorous geese and vegetation quality; specifically, earlier receding water decreased the food availability of *Carex* spp. vegetation, which ultimately influenced herbivorous geese abundance and distribution (Guan et al. 2016, Zou et al. 2017, Zhang et al. 2021a). The elevation distribution of *Carex* spp. vegetation in the study area is generally similar to the height of the dykes, and the dykes have a limited effect on delaying the germination and growth of *Carex* spp. vegetation, which may be the reason for the non-significant change in food quality (NDVI) in the dyke-demolished and preserved areas before and after the dykes were demolished (Fig. 3). However, the present study demonstrated that the wetland vegetation reached the maximum NDVI in almost the same number of days when surrounded by dykes, but the maximum number of days was significantly earlier after the demolition of the dyke (Fig. 3), resulting in a decreased area of suitable habitat for geese, which ultimately influenced geese abundance and distribution (Fig. 4-5). Similar results were also obtained in a recent study (Liang et al. 2021). Future research will focus on the reasons why the abundance of bean geese decreased in the demolished dyke-demolished areas and the abundance of lesser white-fronted geese increased.

This study focused on the factors related to the food resources of waterbirds, but not on the effects of interannual variation in hydrological regimes, climate change, and human disturbance in Dongting Lake. These factors have been demonstrated to influence the habitat selection and spatial and temporal distribution of waterbirds (Yuan et al. 2014, Adam et al. 2015, Wang et al. 2019), and will be considered in future work.

**5. Conclusion and implications**

Habitat suitability and accessibility for waterbirds depend on water level fluctuations, especially in periodically flooded wetlands (Baschuk et al. 2012, Li et al. 2019). Our study demonstrated that dyke demolition resulted in a significant reduction in wetland water areas under the same water level conditions. Furthermore, the large water area maintained in the dyke preserved areas over a long period further demonstrated the importance of the function of the dyke in storing water at low water levels.

The goal of dyke demolition is to interconnect the Dongting Lake hydraulic regime and restore its natural properties. This study only analyzed the effects of dyke demolition on wintering waterbird diversity and habitat factors, but it is unclear whether these effects have a cascading effect on the entire wetland ecosystem. Our results showed that the species and number of wintering waterbirds in the dyke-demolished areas (Chunfeng Lake, Junshanhou Lake, and Hongqi Lake) declined year by year after the demolition of the dyke, while the dyke preserved areas (Daxiaoxi lake and Dingzi dyke) showed an increasing trend. Meanwhile, the high temporal variability in species turnover and species reordering underscores the importance of long-term studies for our understanding of waterbird dynamics. Understanding the effects of water level fluctuations and adaptive water level management on waterbirds and vegetation communities at Dongting Lake can be facilitated by long-term studies. Future studies should prioritize strengthening the frequency of waterbird surveys, conducting ecological restoration in the dyke-demolished areas, and protecting and maintaining the dyke-preserved areas.

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**DATA ACCESSIBILITY**

Relevant data in this study will be available via Dryad: https://doi.org/10.5061/dryad.fn2z34tvm

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