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Original paper

Synergistic succession of the small mammal community and herbaceous vegetation after reconverting farmland to seasonally flooded wetlands in the Dongting Lake Region, China

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Abstract. We investigated the synergistic succession of the small mammal and herbaceous communities after farmland was reconverted to seasonally flooded wetlands in the Dongting Lake Region of China. The composition of small mammals and the herbaceous community was examined in four habitat types: F (farmland), S (where agriculture continued, but human habitation ceased), R (farmland reconverted back to seasonally flooded wetlands), and B (aboriginal seasonally flooded wetlands). Using various diversity indices, the data showed that the small mammal community changed in parallel with the succession of the herbaceous community. Compared to F, there was little change in S, whereas R noticeably changed. *Microtus fortis* inhabited R, because *Carex* spp. was the dominant plant species. R held a mixture dominant species from both F and B, demonstrating that R was in transition (intermediate stages of succession) from F to B. However, the status of the small mammal community in B changed in 2008–2010, due to the operation of the Three-Gorge Reservoir (TGR). In conclusion, our observations demonstrate that the succession of the small mammal community in habitats R and B are directly influenced by human activity in the region, with monitoring being required to continue documenting these changes.

Key words: Dongting Lake region, land reconversion, plant community, small mammal, synergistic succession.

Ecosystem-based disaster risk reduction (Eco-DRR) is sustainable management, conservation, and restoration of ecosystems to reduce the risk of disaster, with the aim to achieve sustainable and resilient development. Eco-DRR represents a type of ecosystem management that provides the opportunity to strengthen natural infrastructure against hazard impacts, in addition to generating a range of social, economic, and environmental benefits for multiple stakeholders. Since 1998, Eco-DRR-based measures of reconverting farmland back to seasonally flooded wetlands have been implemented in the middle reaches of the Yangtze Valley of China, with the objective of restoring the wetland ecology system of lakes, preventing flood disasters on adjoining farmland, and improving the living conditions of people inhabiting this region.

Since the Tang and Song dynasties, Chinese people have been reclaiming wetlands, including sandbars and beaches along rivers and/or entire lakes, through the use of dikes to form polders (floodplain/lowland farmland) to feed the increasing human population. Today, polders are essential for agricultural production in the Dongting Lake region of China. Although reclamation has greatly contributed to increasing grain supply and alleviating tension between the expanding population and land shortage historically, it has led to an increase in the number of regional flood disasters (particularly by the end of the 20th century) (Xie et al. 2014). This issue exists because there are insufficient wetlands remaining to receive and

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store floodwater, purify water, and maintain biodiversity. Consequently, in 1998, the Chinese government implemented a scheme to reconvert some farmland on polders back to seasonally flooded wetlands in the Dongting Lake region (Xie et al. 2014). The land was converted back to wetland habitat in two ways: (1) Farmland that was reconverted back to seasonally flooded wetlands, in which human habitation was removed from polders and all associated agricultural activity was stopped (R), and (2) Single restoration farmland, in which only human habitation was removed from polders, but agricultural activity continued (S). Following reconversion, S polders are not submerged during the flood (or rainy) season, whereas R polders are submerged every year (from May to October when 70–90% of the total annual precipitation occurs) (Xie et al. 2014). However, S polders are covered by floodwater (as flood discharge area) when lakes and rivers can no longer contain large amounts of water, with this phenomenon threatening protected polders during the flood season of some years.

After reconversion, animal and plant communities inhabiting these areas should change in response to the changing environment. This is because species composition in a community responds to changes in disturbance (Hobbs and Huenneke 1992). For instance, in habitat R, which was reconverted from farmland to seasonally flooded wetlands, animal and plant communities should respond to annual flooding, which cannot be eliminated by artificial management. First, plants must adapt to flooding, as flooding is essential in structuring plant communities on the beaches of rivers and lakes. For example, in Sweden, river-margin vegetation responded differently to different types of regulated water-level regimes (Jansson et al. 2000). In theory, the structure of vegetation should reflect how wildlife species are distributed, with the succession of the small mammal community following changes to the vegetation community (Thompson and Gese 2013). In natural ecological systems, plants provide a source of food, while the microclimate of vegetation influences the activity of small mammals. In turn, the feeding preferences of these mammals is expected to affect the structure of the vegetation community. Small mammals, especially rodents, are directly and indirectly associated with plants. For example, in the Baiyinxile typical steppe of Inner Mongolia, rodent diversity is positively correlated with the plant community, the evenness index of rodents is positively correlated with plant evenness, and rodent species diversity is negatively correlated with the height of the herb layer and the percentage of vegetation cover (Zhou et al. 1982). In the Dongting Lake area, the reed vole, *Microtus fortis*, which is an herbivorous rodent, mainly inhabits and reproduces on beaches covered by herbaceous vegetation (Wu et al. 1996; Chen et al. 1998; Wu et al. 1998). The lakeside beaches are usually covered with heavy sedge (*Carex* spp.), which is the preferred food item of this vole species (Wu et al. 1998). The other main small mammal species in the Dongting Lake area include the brown rat *Rattus norvegicus*, the Tanezumi rat *Rattus tanezumi*, the striped field mouse *Apodemus agrarius*, and the house mouse *Mus musculus*, all of which mainly feed on plant seeds (Chen et al. 1998). Thus, it is likely that the succession of small mammals after converting farmland back to seasonally flooded wetlands is correlated with vegetation community succession.

Recent studies have already investigated how small mammal or vegetation communities have changed after the reconversion project was initiated in the Dongting Lake region (Zhang 2006; Zhang et al. 2009, 2012, 2013; Ren et al. 2011). Four habitat types have been delineated in this area; namely, F (farmland), S (where agriculture continued, but human habitation had ceased), R (farmland reconverted back to seasonally flooded wetlands), and B (aboriginal seasonally flooded wetlands). The species diversity of the herbaceous community in habitat S is similar to that characterized in normal farmland. In comparison, the herbaceous community in habitat R has changed significantly, supporting lower species abundance than that in typical farmland. In parallel, the species diversity of habitat R differs from that found on the beach (i.e., the climax herbaceous community is adapted to submergence in summer). A similar pattern has been detected for the small mammal community, with a minimal change in habitat S, but a noticeable change in habitat R (Zhang et al. 2013). These studies demonstrated that the reconversion project has caused changes to the diversity of plant communities and small mammals. More importantly, the population explosion of *M. fortis* in the Dongting Lake region has led to the small mammal community being focused on in this region (Zhang et al. 2007b). The changes in the plant community of habitat R might have influenced the changes in small mammal community, because the preferred vegetation of *M. fortis*, which dominates the habitat of aboriginal seasonally flooded wetlands, is the main reason why voles has proliferated. The major food items of voles are *Carex* spp. in spring (71.05%) and winter (68.97%) when they occupy this habitat type (Wu et al. 1998). Thus, the small mammal community might be particularly sensitive to these changes due to their energetic demands and the balance between foraging efficiency and security (Thompson and Gese 2013). However, no studies have analyzed how conversion has affected the small mammal and plant communities in combination. Thus, the present study aimed to investigate how the biological community (small mammals and herbaceous community) changed in polders after reconverting farmland back to seasonally flooded wetlands. Specifically, we aimed to identify the co-succession of the small mammal community with the plant community during the conversion of farmland back to lakeside beach habitat (seasonally flooded wetlands). Our results are expected to demonstrate the co-dependence of these two groups in restored landscapes, which might provide information towards enhancing restoration programs of lake and river habitats.

Materials and methods

Study site

The Dongting Lake region is located in the middle reaches of the Yangtze Valley and the northern part of Hunan Province, China (28°30'–30°20'N and 111°40'–113°10'E). The region is subtropical, with four defined seasons. The weather is warm and humid, with a mean annual temperature of 16–17°C and a mean annual rainfall ranging from 1200 to 1550 mm. Over the period of a year, precipitation is asymmetrical, with 70–90% of the total annual precipitation occurring in the rainy season, which extends from May to October (also called the flood season). Dongting Lake is one of the most important regions for agricultural production in the Yangtze Valley.

Four typical habitats were selected for the current study in the Dongting Lake region, namely F, S, R, and B (Table 1). According to the land use situation, seven sites were selected to conduct a census of the small mammal community from April 2003 to January 2006 (the first sampling period). Among these sites, the sampling site on a hilly woodland surrounding the lake was not a farmland, and so was excluded from the analysis (Fig. 1). However, a sampling site (B2) on the lake beach was added, and a sampling site S1 was replaced with S2 between January 2008 and October 2010 (the second sampling period). In the end, eight sampling sites were used in the study area (Fig. 1, Table 1). The herbaceous communities were checked in 2005 and 2009. All survey areas fell within the alluvial plain region of Dongting Lake, and were situated at an altitude of approximately 25–30 m above sea level.

The normal farmland sites were F1 and F2 (Table 1). The main crops include paddy rice, cotton, soybean, ramie, and maize in this region during summer and fall. In winter, the farmland is largely unused, except for plant rape and astragalus. F1 and F2 only have trees interspersed among farmhouses and along some highways,

Table 1. Habitat types and sampling sites in the Dongting Lake region

Habitat types	Sample habitat sites	Characteristics
F: normal farmland	F1: Anzhao polder in Anxiang County (29°29.5'N, 112°11.4'E); F2: Matang Polder in Yueyang County (29°14.9'N, 113°04.7'E)	The type of habitat was typical farmland near inhabited villages protected by dikes in flood season, resulting in major human interference.
S: single restoration farmland	S1: Linan polder in Lixian County (29°35.6'N, 111°47.6'E); S2: Chuanye polder in Yuanjiang County (28°59.6'N, 112°15.1'E); S3: Weidihu polder in Hanshou County (28°57.5'N, 111°58.1'E)	After reconversion in 1998, farmland continued to be used as farmland, but the village was removed; thus, only agriculture represented the main form of human interference.
R: farmland that was reconverted back to seasonally-flooded wetlands	R: Xiaojichen polder of Huarong County (29°40.7'N, 112°56.5'E)	Human habitations were removed from the polder and associated agricultural activities were stopped after reconversion in 1998, there were less interference than habitat F and S.
B: natural or aboriginal beach (natural seasonally-flooded wetlands)	B1: the natural beach sites include long stretches of beach in the vicinity of Matang polder (Site F2) in Yueyang county (29°14.5'N, 113°03.2'E); B2: the beach in the vicinity of Beizhuzhi Town, Datonghu County (29°10.1'N, 112°47.7'E).	The natural beach sites were at the final stage of succession (i.e., mature/climax community) and covered by water in flood season with the lowest human interference out of all the study sites.

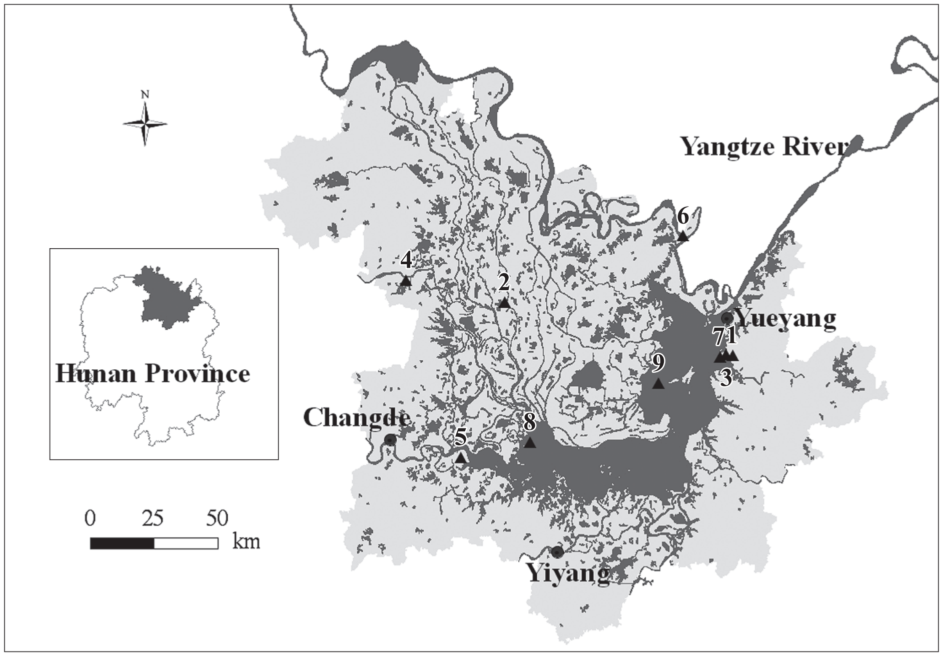

Fig. 1. Sampling sites in the Dongting Lake region, Hunan, China. Nine sampling sites were established in the study area. Site 1 is a hilly woodland surrounding the lake, not a farmland, and so was excluded from the analysis in this study. Site 2 (= habitat F1) and site 3 (= habitat F2) were typical farmland in a protected polder. Site 4 (= habitat S1), site 8 (= habitat S2), and site 5 (= habitat S3) were habitat S where only human habitation was removed from polders, but agricultural activity continued. Site 6 (= habitat R) was habitat R where human habitation was removed from polders and all associated agricultural activity was stopped. Site 7 (= habitat B1) and site 9 (= habitat B2) were natural seasonally-flooded wetlands in the final stages of succession.

with no densely wooded areas. F1 and F2 contain wide drains or feeder canals. All six townships in F1 (encompassing 20 500 ha territory, 10 300 ha farmland, and more than 170 000 people) were inundated by summer floods from July to October of 1998 after the south riverbank burst. A population of *M. fortis* migrates into the farmland of Matang polder (F2) during the flood season each year, because it contains a long stretch of beach extending out of the dike. F1 and F2 represent two different types of rodent pest areas, allowing the small mammal communities inhabiting the farmlands surrounding the Dongting Lake area to be divided into two types, based on dominant species: (1) the *R. norvegicus* and *A. agrarius* pest area, and (2) the *M. fortis* pest area (Chen et al. 1988).

The sites in habitat S included S1, S2, and S3 (Table 1). Habitat S1 was a single restoration farmland that was investigated from 2003 to 2006, and included 3700 ha territory, with two towns containing 19 administrative villages and approximately 28 400 people before reconversion. After reconversion, the polder continued to be used to plant rice and cotton in summer, while it was planted with rape in winter or left fallow. Habitat S2 was a single restoration farmland that was investigated from 2008 to 2010. It included one town containing six villages and nearly 4000 people, encompassing an area of 1100 ha before reconversion. After reconversion, the original six villages were combined into two villages. Rice (summer) and rape (winter) were primarily planted on the farmland, in addition to planting poplar. Habitat S3 was also a single restoration farmland, with poplar (*Populus* spp.) being planted on most of the polder (approximately 3400 ha territory), with some vegetable crops under the poplar and fallow land. Compared with S1 and S2, S3 contained more wooded areas, and was subject to less interference by farming activity.

Habitat R was a site that was reconverted back to seasonally flooded wetlands from farmland (Table 1). The polder covered 2400 ha, including one town with nearly 11 400 people before reconversion. The polder was surrounded by water in the flood season before reconversion. After reconversion in 1998, the land was used to plant poplar (*Populus* spp.), silvergrass (*Triarrhena* spp.), and reeds (*Phragmites* spp.), or was left fallow, and was covered in water during the flood season. This habitat is occupied by fewer people, with low numbers of livestock and low levels of farming activity, resulting in it being subject to less interference than the sites in habitats F and S.

The natural beach sites included B1 and B2 (Table 1). Habitat B1 is covered in *Carex* spp. and *Polygonum hydropiper*, with the lowest human interference out of all the study sites. Habitat B2 was added as a study site from 2008 to 2010. Habitat B2 contains *Triarrhena* spp., *Phragmites* spp., and *Populus* spp, in addition to *Carex* spp. and *P. hydropiper*. Thus, B2 is subject to more interference than B1, due its proximity to human activity during the planting and harvesting season.

The B1, B2, and R habitats are covered by water during the flooding season in typical years (i.e., for approximately 3–5 months for B1 and B2, approximately one month for R, because it is at a higher altitude than B1 and B2). Dikes (levees) are present around the F1, F2, S1, S2, and S3 habitats and adjacent to the lake or river to protect local residents and their farmland and houses from flooding. However, S1 was covered with flood discharge in 2003 when the water levels of the lake and river were too high, threatening the protected polders.

The striped field mouse *A. agrarius* is the dominant species in farmland, with common species, including the Norway rat *R. norvegicus*, Tanezumi rat *R. tanezumi*, house mouse *M. musculus*. Other species of low abundance include the lesser rice field rat *Rattus losea*, sulphur-bellied rat *Niviventer confucianus*, Himalayan rat *Rattus nitidus*, and harvest mouse *Micromys minutus* (Chen et al. 1988). With the flooding of beaches being a natural occurrence during the wet season, *M. fortis* was the only known dominant species inhabiting the beach before, and its development was closely related to evolvement of lake beaches in Dongting Lake (Zhang et al. 2014). When the beaches flooded during the wet season, the voles would migrate to the surrounding farmlands. When the lake beach emerged in dry season, the voles returned to the beach (Guo et al. 1997). In some years, the vole population caused serious crop damage after it moved to the farmland (Chen et al. 1998).

Trapping of small mammals

Snap traps (150 × 80 mm, Guixi Mousing Tool Factory, Jiangxi, China) were used on all habitats throughout the census. Trapping sessions were separated into two periods: April 2003–January 2006 and January 2008–October 2010. Although the census on habitat B1 (beach) and habitat F3 (farmland) was continuous, there was no continuity in the other habitats. Furthermore, the impact of the Three-Gorge Reservoir (TGR) activity on small mammals was evident during the second period (Zhang et al. 2014). After the completion of the Three Gorges project in 2009, the water storage level went to 175 m and a huge reservoir was formed with a total area of 1084 square kilometers and storage capacity of 39.3 billion m^3, which is located in the upstream of the Yangtze River at the boundary of Chongqing municipality and Hubei province. Thus, the data were analyzed separately based on these two periods. Trapping was carried out four times a year (winter in January, spring in April, summer in July, and fall in October). If the habitats B1 and B2 (beach) or R were submerged during the wet season, surveys were not conducted in summer (July). Traps, baited with fresh sunflower seeds, were placed on the ground in the afternoon, and then, collected the next morning. One treatment at one site covered a single night. Three or four plots of approximately 6–10 ha each were sampled in each habitat (i.e., F1, F2, S1, S2, S3, R, B1, and B2) of each study site. Approximately 80–100 traps were set in each plot; so, a total of 200–300 trap nights was completed in each habitat for each treatment at each site. Traps were spaced approximately 5 m apart along the field ridges of farmland or along a line-transect on the beaches. Captured animals were transferred to the laboratory and identified.

Plant community

Herbaceous plants are the main vegetation type in the farmland margins and in the area of farmland reconversion in Dongting Lake Plain (in addition to crops and tree or shrub plantations planted for economic purposes). Thus, this study focused on documenting annual and perennial herbaceous plants. For this reason, various crops in different land use types (such as poplars and reeds on the beach habitat) were excluded from the analyses. Grassland and herbaceous communities were analyzed at the same sites as the small mammal surveys. Survey was conducted in January (winter), April (spring), July (summer), and October (fall) in 2005 and 2009.

Four plots of approximately 6–10 ha each were sampled at each sampled site, in the same area where the small mammal community census was conducted. A total of five quadrats of 1 m^2 was established in each plot, i.e., 20 quadrats of 1 m^2 (= 5 sample quadrats × 4 plots) for each treatment in each sampled site. In habitats B and R, five sampling areas were established in the center and diagonally across each plot, with 50-m spacing. In the farmland, ten sampling areas of 1 m^2 were established along the ridge (field margin). The other ten samples were placed among fields in the survey center of the small mammal community plots, with at least 100 m spacing and in different fields. The height, cover, and abundance of plants were recorded. Based on mean square value sampling, the relative dominance of species and the diversity index were calculated for each community.

Analysis of small mammal community diversity

The relative population abundance of the small mammal community was indicated by trap success and was calculated as the percentage capture success in 100 traps: $D = (100\ N/T) \times 100\%$, where D is the relative population abundance, N is the number of animals caught by all traps, and T is all traps collected the next morning. The dominant concentration index (C) and degree of dominance (I) were calculated using Simpson's formula (1949): $C = \sum (Ni/N)^2$, $I = Ni/N$, where Ni is the number of animals per species and N is the number of animals. The Shannon-Wiener diversity index (H') was calculated using the equation (Peet 1974): $H' = -\sum_{i=1}^{s} Pi \ln Pi$, where S is the number of species, with $Pi = N_i/N$, where N_i is the number of species i and N is the number of animals. The evenness index (E) was calculated following Pielou (1966): $E = H'/lnS$.

Importance value of herbaceous plants

The importance value (IV) is an integrated quantity index that shows the status and function of a single species in the community. This index (range: 0–100) shows the relative importance of a plant species according to its relative frequency, relative coverage, and relative height. It is a comparative statistic that shows the status, function, and authenticity of a species. The importance value of herbaceous plants was calculated as follows: $IV = [(RFE + RCO + RHI)/300] \times 100\%$, where RFE is the relative frequency, RCO is the relative coverage, and RHI is the relative height. The relative frequency (RFE) was calculated by $RFE = (F_i/\sum F_i) \times 100\%$, where F_i is the frequency of species i: $F_i = (Q_i/\sum Q) \times 100\%$; Q_i is number of quadrats where species i appeared, $\sum Q$ is number of all quadrats, and $\sum F_i$ is the total frequency of all species. The relative coverage (RCO) was calculated by $RCO = (C_i/\sum C_i) \times 100\%$, where C_i is the average coverage of species i. $C_i = (C'_i/A) \times 100\%$; C'_i is the total crown area of species i, A is the horizontal area of the total quadrat, and $\sum C_i$ is the total average coverage of all species. Relative height (RHI) was calculated by $RHI = (H_i/\sum H_i) \times 100\%$, where H_i is the average population height of species i in the natural environment, and $\sum H_i$ is the total average height of all species.

Analysis of herbaceous community diversity

The species richness index is shown by species number (S). The dominant concentration index (C) was calculated using Simpson's formula (1949): $C = \sum (IV_i/IV)^2$, where IV_i is the importance value of each species, and IV is the total importance of all species. The Shannon-Wiener diversity index (H') was calculated using the equation (Peet 1974) $H' = -\sum_{i=1}^{s} Pi \ln Pi$, where S is the number of species, with $Pi = IV_i/IV$, where IV_i is the importance value of per species and IV is the total importance of all species. The evenness index (E) was calculated following Pielou (1966): $E = H'/lnS$.

Results

Biodiversity indices of the small mammal community

Between 2003 and 2006, the 29 081 traps set in the four habitat types caught 753 animals (including evidence of 25 animals that were caught but escaped from traps, such as tails, claws, bloodstains, and hair), representing nine species. Among them, *A. agrarius* and *M. fortis* were the dominant species (representing 53.98% and 39.84% of the total species composition, respectively), followed by *R. norvegicus* (3.02%), the European hedgehog *Erinaceus europaeus* (1.65%), the Asian house shrew *Suncus murinus* (0.69%), *R. tanezumi* (0.27%), *M. musculus* (0.27%), *R. losea* (0.27%), and the chestnut white-bellied rat *Nivieter fulvescens* (0.14%). Between 2008 and 2010, the 24 928 traps set in the seven habitat types caught 1322 animals (including evidence of 45 animals), representing nine species. *A. agrarius* (30.23%) and *M. fortis* (65.54%) were still the dominant species, followed by *R. norvegicus* (1.88%), *S. murinus* (1.64%), *E. europaeus* (0.23%), *R. tanezumi* (0.16%), *M. minutus* (0.16%) *M. musculus* (0.08%), and *R. losea* (0.08%). The biodiversity indices are shown in Table 2.

Biodiversity indices of the herbaceous community

The species diversity characteristics of the herbaceous community have been previously described by Zhang et al. (2013) (Table 3). The species abundance, the dominant concentration index, the Shannon-Wiener diversity index, and the evenness index indicated that the herbaceous community in habitat S remained similar to that in normal farmland (habitat F). In comparison, there was a noticeable decline in the species abundance of the herbaceous community in habitat R compared to that of normal farmland (habitat F). Species abundance of the plant communities in habitat S and R also differed from

Table 2. Biodiversity indices of the small mammal communities

Habitats	2003–2006				2008–2010			
	Numbers of species	Dominant concentration index	Shannon-Wiener index	Evenness index	Numbers of species	Dominant concentration index	Shannon-Wiener index	Evenness index
F1	5	0.43	1.12	0.70	2	0.56	0.64	0.92
F2	6	0.58	0.82	0.46	6	0.52	0.96	0.54
S1	4	0.88	0.30	0.22	–	–	–	–
S2	–	–	–	–	6	0.49	0.93	0.52
S3	3	0.68	0.55	0.50	2	0.90	0.21	0.30
R	4	0.56	0.73	0.53	4	0.82	0.41	0.29
B1	2	0.92	0.18	0.26	5	0.96	0.12	0.07
B2	–	–	–	–	5	0.46	0.87	0.54

F1 and F2 habitats were normal farmland in protected polders. *Microtus fortis* migrates to habitat F2 during the flood season, due to the presence of a long stretch of beach from the dike near the habitat.
S1, S2, and S3 habitats were single restoration farmland. S1 (sampled from 2003 to 2006) and S2 (sampled from 2008 to 2010) were still farmland. Most of S3 had been planted with one species of poplar (*Populus* spp.).
Habitat R was a polder that was reconverted back to seasonally-flooded wetlands from farmland, and was planted with poplar (*Populus* spp.), silvergrass (*Triarrhena* spp.), and reeds (*Phragmites* spp.), or left fallow, and was covered in water during the flood season.
Habitat B1 was a natural beach (seasonally-flooded wetlands) on the lake in the final stages of succession (climax community), and was covered *Carex* spp. and *Polygonum hydropiper*; Habitat B2 was added to the study from 2008 to 2010, and was also a natural beach, which was covered with *Triarrhena* spp., *Phragmites* spp., and *Populus* spp., in addition to *Carex* spp. and *Polygonum hydropiper*.
The same information applies for Table 3, 6, and 8.

that of the natural beach habitat B (a climax herbaceous community adapted to submergence in water during the summer floods). The characteristics of the herbaceous community in habitat R changed with the season, being similar to that of the natural seasonally flooded wetlands in fall at the end of summer flooding, but also being similar to that of the typical farmland during the spring before flooding.

Correlations between the small mammal and herbaceous communities, 2003–2006

Correlations between the biodiversity indices of the small mammal community in 2003–2006 and the herbaceous community in 2005 were investigated with Pearson's correlation coefficient using 23 pairs of the data (five habitats for four seasons and one habitat for three seasons). This analysis showed that the number of small mammal community species was significantly positively correlated with the number of herbaceous species, as well as the Shannon-Wiener and the evenness indices of the herbaceous community (Table 4). In contrast, the number of small mammal species was significantly negatively correlated with the average coverage of the herbaceous community and the dominant concentration indices (Table 4), with fewer mammal species being present when the dominance of herbaceous plants was higher.

The correlation coefficients indicated that habitats with higher diversity carried more animal species. This correlation might be primarily due to vegetation serving as the main food source for small animals. Compared with farmland habitat F and S, the number of herbaceous species was lower in habitat R, but was higher than that in the natural seasonally flooded wetlands of habitat B (Table 3). The same trend being detected for the number of small mammal species (Table 2).

Correlations between the small mammal and herbaceous communities, 2008–2010

The trend in the number of small mammal species and herbaceous species that was detected in 2008–2010 was similar to that detected in 2003–2006; however, some differences were present. Correlations between the biodiversity indices of the small mammal community in 2008–2010 and the herbaceous community in 2009 were investigated with Pearson's correlation coefficient using 26 pairs of the data (five habitats for four seasons and two habitats for three seasons). This analysis showed that the number of small mammal species had no significant correlation with the number of herbaceous species, the dominant concentration index, the Shannon-Wiener index, the evenness index, or the average coverage of the herbaceous community (Table 5). In contrast, the success rates of small mammal traps were significantly correlated with all indices (Table 5). This result indicated that small

Table 3. Biodiversity indices of the herbaceous community in different habitats and seasons (reformed from Zhang et al. 2013)

Habitats	Seasons	2005				2009			
		Numbers of species	Dominant concentration index	Shannon-Wiener index	Evenness index	Numbers of species	Dominant concentration index	Shannon-Wiener index	Evenness index
F1	Spring	46	0.0449	3.34	0.87	45	0.0550	3.22	0.85
	Summer	51	0.0455	3.43	0.87	39	0.0809	2.97	0.81
	Fall	52	0.0516	3.38	0.86	56	0.0405	3.52	0.88
	Winter	35	0.0512	3.23	0.91	42	0.0441	3.38	0.90
F2	Spring	51	0.0442	3.48	0.88	38	0.0949	2.88	0.79
	Summer	51	0.0459	3.46	0.88	47	0.0515	3.34	0.87
	Fall	44	0.0536	3.28	0.87	47	0.0432	3.42	0.89
	Winter	33	0.0702	3.01	0.86	28	0.0933	2.71	0.81
S1	Spring	48	0.0444	3.38	0.87	–	–	–	–
	Summer	49	0.0432	3.44	0.88	–	–	–	–
	Fall	59	0.0493	3.46	0.85	–	–	–	–
	Winter	40	0.0472	3.28	0.89	–	–	–	–
S2	Spring	–	–	–	–	56	0.0346	3.65	0.91
	Summer	–	–	–	–	54	0.0476	3.44	0.86
	Fall	–	–	–	–	67	0.0354	3.70	0.88
	Winter	–	–	–	–	38	0.0572	3.16	0.87
S3	Spring	53	0.0403	3.51	0.88	50	0.0508	3.34	0.85
	Summer	56	0.0376	3.59	0.89	44	0.0498	3.30	0.87
	Fall	56	0.0497	3.40	0.84	59	0.0395	3.64	0.89
	Winter	48	0.0450	3.39	0.87	46	0.0454	3.41	0.89
R	Spring	46	0.0620	3.18	0.83	39	0.0574	3.15	0.86
	Summer	33	0.0852	2.81	0.80	26	0.1174	2.53	0.78
	Fall	16	0.1377	2.31	0.83	25	0.1336	2.52	0.78
	Winter	26	0.1485	2.40	0.74	27	0.1326	2.61	0.79
B1	Spring	17	0.1712	2.10	0.74	15	0.2462	1.78	0.66
	Summer[a)]	–	–	–	–	–	–	–	–
	Fall	13	0.2320	1.77	0.69	8	0.3365	1.34	0.64
	Winter	13	0.2649	1.70	0.66	9	0.3381	1.40	0.64
B2	Spring	–	–	–	–	17	0.2423	1.93	0.68
	Summer	–	–	–	–	–	–	–	–
	Fall	–	–	–	–	11	0.3269	1.50	0.63
	Winter	–	–	–	–	16	0.2892	1.72	0.62

[a)] There were no data in summer because the beach by the lake was covered with water.

mammal density in each habitat was correlated with the dynamics of the herbaceous community.

Correlations between key species of the small mammal and herbaceous communities

The success rates of the traps for small mammal species and their relative percentage out of total species composition (Table 6) showed that *A. agrarius* and *M. fortis* were the dominant species. These two species represented over 60% of the total species; thus, we analyzed these two species in relation to the herbaceous community.

Apodemus agrarius was recorded in all studied habitats and was one of the dominant species in all habitats, except B1 (Table 6). The density of *A. agrarius* was low in the natural seasonally flooded wetland habitat before the operation of the TGR, but became one of two dominant species (*M. fortis*) after the onset of TGR operation (Zhang et al. 2014).

Correlations between the trapping indices of *A. agrarius* and the herbaceous community were investigated with

Table 4. Correlations between small mammal communities from 2003 to 2006 and plant communities in 2005

			Small mammal community				
			Numbers of species	Trap success (%)	Dominant concentration index	Shannon-Wiener index	Evenness index
Herb community	Numbers of species	r	0.463	–0.398	–0.018	0.150	–0.413
		P	0.023	0.054	0.932	0.485	0.045
		N	23	23	23	23	23
	Dominant concentration index	r	–0.580	0.320	0.113	–0.243	0.375
		P	0.004	0.136	0.608	0.265	0.078
		N	23	23	23	23	23
	Shannon–Wiener index	r	0.570	–0.410	–0.068	0.209	–0.374
		P	0.005	0.052	0.756	0.339	0.079
		N	23	23	23	23	23
	Evenness index	r	0.593	–0.372	–0.111	0.244	–0.361
		P	0.003	0.080	0.616	0.261	0.090
		N	23	23	23	23	23
	Total frequency	r	0.156	–0.229	0.136	–0.039	–0.309
		P	0.478	0.293	0.537	0.859	0.151
		N	23	23	23	23	23
	Average coverage (%)	r	–0.763	0.134	0.304	–0.417	0.098
		P	<0.001	0.541	0.158	0.048	0.658
		N	23	23	23	23	23
	Average Height	r	–0.170	–0.030	0.122	–0.101	–0.129
		P	0.438	0.894	0.579	0.646	0.559
		N	23	23	23	23	23

Table 5. Correlations between small mammal communities from 2008 to 2010 and plant communities from 2009

			Small mammal community				
			Numbers of species	Trap success (%)	Dominant concentration index	Shannon-Wiener index	Evenness index
Herb community	Numbers of species	r	–0.223	–0.754	–0.241	0.245	0.405
		P	0.274	<0.001	0.235	0.228	0.040
		N	26	26	26	26	26
	Dominant concentration index	r	0.269	0.908	0.195	–0.226	–0.417
		P	0.184	<0.001	0.341	0.266	0.034
		N	26	26	26	26	26
	Shannon-Wiener index	r	–0.262	–0.853	–0.222	0.239	0.423
		P	0.195	<0.001	0.277	0.240	0.031
		N	26	26	26	26	26
	Evenness index	r	–0.272	–0.896	–0.151	0.180	0.374
		P	0.179	<0.001	0.463	0.379	0.060
		N	26	26	26	26	26
	Total frequency	r	–0.305	–0.799	–0.053	0.070	0.294
		P	0.129	<0.001	0.798	0.733	0.145
		N	26	26	26	26	26
	Average coverage (%)	r	0.101	0.444	0.461	–0.419	–0.606
		P	0.625	0.023	0.018	0.033	0.001
		N	26	26	26	26	26
	Average Height	r	–0.028	0.475	0.356	–0.385	–0.411
		P	0.893	0.014	0.074	0.052	0.037
		N	26	26	26	26	26

Table 6. Population of *Apodemus agrarius* and *Microtus fortis* in each habitat

Habitats	Trap success (%)						Percentage in species composition (%)			
	2003–2006			2008–2010			2003–2006		2008–2010	
	All species[a)]	*A. agrarius*	*M. fortis*	All species[a)]	*A. agrarius*	*M. fortis*	*A. agrarius*	*M. fortis*	*A. agrarius*	*M. fortis*
F1	0.57	0.28	0.00	0.15	0.08	0.00	60.87	0.00	66.67	0.00
F2	2.09	0.41	1.49	2.13	0.34	1.38	20.14	72.92	17.07	69.51
S1	1.14	0.96	0.00	–	–	–	93.75	0.00	–	–
S2	–	–	–	2.36	0.67	1.43	–	–	29.58	63.38
S3	1.47	1.12	0.00	0.91	0.68	0.00	80.70	0.00	94.74	0.00
R	8.73	6.10	2.30	1.43	1.28	0.07	70.25	26.45	90.63	4.69
B1	2.46	0.10	2.21	11.29	0.03	10.68	4.30	95.70	0.23	98.12
B2	–	–	–	15.86	6.90	7.97	–	–	44.44	51.31

[a)] Including evidence of escaped animals, such as tails, claws, bloodstains, and hair.

Table 7. Correlations between the trapping indices of *Apodemus agrarius* and herbaceous community (excluding habitat B1)

	Year	Index	Item	Herb communities: Numbers of species	Dominant concentration index	Shannon-Wiener index	Evenness index	Total frequency	Average coverage (%)	Average height
A. agrarius	2005	Trap success	r	–0.626	0.793	–0.793	–0.782	–0.219	0.289	0.442
			P	0.003	<0.001	<0.001	<0.001	0.353	0.216	0.051
			N	20	20	20	20	20	20	20
		Dominance	r	0.130	–0.019	0.040	–0.067	0.413	0.378	0.375
			P	0.585	0.936	0.867	0.779	0.070	0.100	0.103
			N	20	20	20	20	20	20	20
	2009	Trap success	r	–0.716	0.937	–0.851	–0.889	–0.700	0.436	0.471
			P	<0.001	<0.001	<0.001	<0.001	<0.001	0.038	0.023
			N	23	23	23	23	23	23	23
		Dominance	r	–0.032	–0.081	0.037	0.086	0.268	0.363	0.349
			P	0.886	0.712	0.867	0.697	0.216	0.089	0.103
			N	23	23	23	23	23	23	23

Pearson's correlation coefficient using 20 pairs of the data in 2005 (five habitats for four seasons) and 23 pairs of the data in 2009 (five habitats for four seasons and one habitat for three seasons). One of them showed that the trap success rate of *A. agrarius* was significantly positively correlated with the dominant concentration index of the herbaceous community, but was significantly negatively correlated with the herbaceous species numbers, the Shannon-Wiener index, and the evenness index (Table 7). These results indicated that lower herb community indices were correlated with higher *A. agrarius* density. However, *A. agrarius* density was also positively correlated with herb coverage and height, suggesting that a flourishing herbaceous community could support a high *A. agrarius* population.

Following reconversion, the characteristics of the herbaceous community indicated that vegetation entered the successional process, transforming from farmland habitat to natural seasonally flooded wetlands (Zhang et al. 2013). The natural seasonally flooded wetlands supported an *M. fortis* breeding colony, with *Carex* spp. representing approximately 50–80% of its diet (Wu et al. 1998). *Carex* spp. is also important for other *M. fortis* activities. Therefore, we analyzed the relationship between the trapping indices *M. fortis* and the population characteristics of *Carex* spp. *Carex* spp. data were obtained for habitat B1, B2, and R (Table 8) in spring, fall, and winter only, because these habitats were submerged in summer. Although *Carex* spp. was the dominant species in habitat R, the importance value of *Carex* spp. in R was still lower than that in the original beach habitat (Zhang et al. 2013).

Table 8. Population characteristics of *Carex* spp. in the habitats R and B

Year	Habitat	Season	Frequency (%)	Average coverage (%)	Average height (cm)	Relative frequency (%)	Relative coverage (%)	Relative height (%)	Importance value (%)
2005	R	Spring	85.0	27.8	44.2	6.0	26.9	13.6	15.5
		Summer	70.0	15.9	46.1	9.0	18.3	14.5	14.4
		Fall	80.0	20.6	49.4	16.8	41.3	27.8	28.6
		Winter	95.0	28.7	50.2	11.4	37.3	41.2	30.0
	B1	Spring	100.0	87.5	28.9	18.9	54.0	19.9	30.9
		Fall	100.0	60.3	24.0	22.2	68.0	23.1	37.8
		Winter	100.0	87.5	26.8	23.8	77.6	33.4	44.9
2009	R	Spring	100.0	33.1	42.4	6.8	28.8	16.0	17.2
		Summer	100.0	47.0	76.4	13.9	41.5	24.1	26.5
		Fall	100.0	51.9	61.4	11.3	49.7	32.7	31.2
		Winter	90.0	34.6	39.8	8.1	51.3	35.7	31.7
	B1	Spring	100.0	76.3	48.6	22.2	70.2	29.4	40.2
		Fall	100.0	67.4	36.2	29.9	74.8	40.1	48.2
		Winter	95.0	79.4	22.68	29.2	85.2	37.4	50.6
	B2	Spring	100.0	83.8	55.55	23.0	83.5	22.5	43.0
		Fall	100.0	74.5	28.1	29.0	88.2	36.9	51.4
		Winter	100.0	63.4	30.6	29.0	84.3	34.2	49.1

Table 9. Correlations between the trapping indices of *Microtus fortis* and the population characteristics of *Carex* spp.

	Year	Index	Item	*Carex* spp.						
				Frequency	Average coverage (%)	Average height (cm)	Relative frequency (%)	Relative coverage (%)	Relative height (%)	importance value (%)
M. fortis	2005	Trap success	r	0.233	0.358	–0.257	0.060	0.017	–0.419	–0.116
			P	0.385	0.174	0.337	0.825	0.950	0.107	0.668
			N	7	7	7	7	7	7	7
		Dominance	r	0.787	0.935	–0.993	0.822	0.916	–0.319	0.770
			P	<0.001	<0.001	<0.001	<0.001	<0.001	0.229	<0.001
			N	7	7	7	7	7	7	7
	2009	Trap success	r	0.203	0.886	–0.560	0.917	0.867	0.463	0.868
			P	0.574	0.001	0.092	<0.001	0.001	0.178	0.001
			N	10	10	10	10	10	10	10
		Dominance	r	0.131	0.807	–0.523	0.834	0.744	0.482	0.776
			P	0.718	0.005	0.121	0.003	0.014	0.159	0.008
			N	10	10	10	10	10	10	10

Correlations between the trapping indices of *M. fortis* and the population characteristics of *Carex* spp. were investigated with Pearson's correlation coefficient using seven pairs of the data in 2005 (one habitat for four seasons and one habitat for three seasons) and ten pairs in 2009 (one habitat for four seasons and two habitats for three seasons). Because *M. fortis* individuals were forced to migrate into habitats F and S by floodwater, the correlation analysis was conducted on habitat R, B1, and B2 only. The dominance of *M. fortis* was significantly positively correlated with the importance value of *Carex* spp. in both 2005 and 2009 (Table 9). This result supported that the beach habitat was suitable for *M. fortis*, due to *Carex* spp. being the preferred vegetation of this species. The correlation coefficient (Table 9) indicated that the frequency and coverage of *Carex* spp. represented the main factors regulating *M. fortis* abundance, while plant height did not matter.

However, the situation in 2009 slightly differed from that in 2005. *Microtus fortis* dominance showed both significantly positive and negative correlations with various *Carex* spp. vegetation indices in both 2005 and

2009. In contrast, the success rates of trapping *M. fortis* were significantly correlated with *Carex* spp. vegetation indices in 2009 only.

Discussion

Our results demonstrate that the characteristics of the small mammal community change in parallel with vegetation succession (reconverting from farmland back to seasonally flooded wetlands), despite obtaining slightly different results in 2005 and 2009. We showed that the composition of herbaceous communities in habitats S1, S2, and S3 remained similar to that of typical farmland (F1 and F2) (Zhang et al. 2013), with a similar result being obtained for small mammals.

Based on the data collected in first investigation period, seasonal submergence of habitat R might have led to the decline in diversity indices of the herbaceous community, with habitat R supporting increasingly fewer species than the farmland (habitat F) following reconversion. The dominant concentration index of the herbaceous community in habitat R was higher than those in farmland (habitat F) and habitat S, especially in fall and winter (Table 3). However, the dominant concentration index of the herbaceous community in habitat R remained lower than that of natural seasonally flooded wetlands (habitat B), especially in spring (Table 3). These results support that habitat R was in the intermediate stage of the succession from farmland to natural lakeside beaches.

If the herbaceous community of habitat B represents the climax community of habitat R succession, fewer mammal species would be detected as the succession process continued. However, during the initial investigation period, the negative correlation between the number of small mammal species and the average coverage of the herbaceous community (Table 4) seemed conflicting, possibly due to the submergence of the natural beach during summer. Under this type of interference, *Carex* spp. were the single dominant species, with *M. fortis* being the only small mammal species adapted to the seasonal flooding of this habitat. *Carex* spp. are not used by humans, nor for livestock and poultry, because of the risk of contracting schistosomiasis. Consequently, *Carex* spp. grow year-round on the beach habitat, with no cutting or grazing disturbance, resulting in high coverage, but low small mammal species numbers, regardless of the frequency and height of herbaceous cover.

The annual flooding of habitat R caused the herbaceous community to change, resulting in it being composed of a mixture of dominant species from both farmland and natural beach habitats. The colonization of habitat R by *Carex* spp. demonstrated that this habitat type was in transition (intermediate stages of succession) between farmland and seasonally flooded wetland habitat, with vegetation composition and dominance changing across seasons (Zhang et al. 2013). In fall, just after floodwater levels dropped, the herbaceous community was similar to that of the natural seasonally flooded wetland habitat, with lower plant species abundance and species diversity and evenness, but a higher concentration of dominant species. In contrast, in spring, the herbaceous community was similar to that of the farmland. The most noticeable change in the small mammal community of habitat R was the use of this habitat for reproduction by *M. fortis*, unlike farmland (Zhang et al. 2009), due to the dominance of *Carex* spp., which is a preferred food of *M. fortis*. Because some herbaceous species in the farmland areas remained in habitat R, *A. agrarius* (the dominant farmland species) was co-dominant with *M. fortis* (Table 6). The correlation analysis between the biodiversity indices of the small mammal and herbaceous communities in 2005 supported a similar decline in species numbers in both communities as vegetation succession progressed towards the climax community (i.e., natural seasonally flooded wetlands), which was characterized by stable community composition, low species abundance, low species diversity and evenness, and a high concentration of dominant species.

However, the results of the 2008–2010 surveys differed from those obtained in 2003–2006. We suggest that this discrepancy was due to the start of TGR operation at the end of 2008. TGR operation reduced the intensity of flood waterlogging in summer (Fu et al. 2010), allowing additional small mammal species to inhabit the lakeside beaches (Zhang et al. 2014). In the second survey (2008–2010), the species composition of the small mammal community on some parts of the beach was similar to that in the farmland habitat, due to large extents of beach remaining dry (Zhang et al. 2014). However, the composition of the herbaceous community still influenced that of the small mammal community. For example, high *A. agrarius* population densities on the seasonally flooded wetlands (e.g., B2) might benefit from high herbaceous community coverage (Table 7).

Reconverting farmland back to lake beaches might also facilitate the reforestation of poplars in the Dongting Lake region (Xie and Chen 2008; Hou et al. 2011). These forests might provide refuges for *A. agrarius*, allowing individuals to escape mortality caused by typical summer floods by climbing trunks or inhabiting trees in habitats situated above the maximum flood level. If *A. agrarius* could occupy alternative nearby sites as refuges, more individuals might survive (Zhang et al. 2007a). This phenomenon has been reported at other wetlands (Stickel 1948; Wetzel 1958; McCarley 1959; Williams et al. 2001). Consequently, B2 contained a greater number of small mammal species than B1, because it had more plant species (including *Triarrhena* spp., *Phragmites* spp., and *Populus* spp.) and was situated at a slightly higher elevation.

During the process of vegetation succession, *M. fortis* increasingly used habitat R, while *A. agrarius* intruded on the beach habitat, demonstrating two important changes. *Microtus fortis* mainly inhabits swamp and lakeside beach habitats containing plenty of *Carex* spp. during the dry season. It preferentially feeds on the tender leaves of *Carex* spp. (Wu et al. 1998). In addition, this species swims well (Zhang 2018), enabling it to cope with the alternate wet and dry environment of the beaches of Dongting Lake. As a result, *M. fortis* is the dominant small mammal species on these beaches. During major floods, *M. fortis* individuals migrate to nearby farmland (Guo et al. 1997), causing serious damage to agricultural production (Chen et al. 1998). After farmland was reconverted back to seasonally flooded wetlands, it was found that the voles were inhabiting habitat R. Thus, habitat R provides the voles with more habitats containing more food (*Carex* spp.) than before, thus facilitating greater fecundity. Therefore, it is more likely that there would be an outbreak of the *M. fortis* population, leading to disasters in Dongting Lake during years when the population peaks. For example, during the 2007 flood season, there was an outbreak in the *M. fortis* population, resulting in it decimating agricultural crops and the surrounding local environment (Zhang et al. 2007b). Thus, it is worth tracking changes in the population dynamics of *M. fortis*.

The intrusion of *A. agrarius* to the beach environment was probably due to the onset of TGR operation in 2008, rather than the conversion of farmland back to beaches. Some studies suggest that *A. agrarius* is a wetland species (Scott et al. 2008; Balčiauskas et al. 2012; Horváth et al. 2012) that dominates the farmlands (wet rice paddies) in the Dongting Lake area (Chen et al. 1988; Wang et al. 2003; Li et al. 2005). Before TGP operation, this species occurred at low densities on the beaches because of persistent submergence during the flooding season, but became universally present afterwards, with a steadily increasing population (Zhang et al. 2014). TGR operation led to longer periods of beach exposure and lower risk of flooding, providing the opportunity for *A. agrarius* to establish home ranges and reproduce during the dry season (Zhang et al. 2014). High herbaceous coverage of the beaches with *Triarrhena* spp., *Phragmites* spp., and *Populus* spp., probably also facilitated its establishment. The high densities of this species on some beaches are of concern, as major floods would force the population to migrate to farmland, leading to the damage/loss of crops and generating a health hazard to humans (Guo et al. 1997). Therefore, it is important to monitor fluctuations in the populations of *A. agrarius*, to mitigate population outbreaks.

However, *A. agrarius* density in habitat B1 was lower than that in habitat B2, because TGP impacted B1 less than B2. The elevation of the B1 habitat was lower than that of the B2 habitat, resulting in it being covered by water for longer periods during the summer flooding season. The B1 habitat was primarily covered by *Carex* spp. and *P. hydropiper*, unlike B2, which was also covered by *Triarrhena* spp., *Phragmites* spp., and *Populus* spp. These species might not grow in B1, because they are more suited to higher altitudes. Consequently, B1 was subject to more flooding and less human impact than B2. Thus, *A. agrarius* might not have migrated to B1 because of severe summer flooding and waterlogging, rather than vegetation cover.

In conclusion, habitat R had noticeably altered, which contained fewer small mammal and herbaceous species than habitat S and F, but more species from both communities than habitat B. This process appeared to be negated by the onset of TGR operation, resulting in some habitat B containing higher numbers of small mammal and herbaceous species than expected, due to greater water control and reduced flooding levels. These changes might lead to outbreaks in *A. agrarius* and *M. fortis* populations, which could negatively impact agricultural crops if major floods occurred, particularly if R habitats are present to support more rodent populations.

As a final note, although this study demonstrates that the small mammal community in habitat R and the natural beach habitat (seasonally flooded wetlands) are directly influenced by human activity in the Dongting Lake region, this study only provides data from sampled habitats over limited periods with low sampling effort; in particular, there was no replication sampling in habitat R. Thus, the results should not be generalized as being representative of lake side habitats beyond our study site. Overall, our results provide important information for animal conservation and applied ecology. Although some studies have assessed the relationship of vegetation structure with wildlife composition, the relationship is often complicated by the fact that local disturbance regimes vary across sites (Thompson and Gese 2013). For example, in the Dongting Lake area, after land reconversion, the effects of TGP operation added a different component to the vegetation-animal relationship. More monitoring is required to continue documenting changes, and to test predictions on small mammal community trends, to elucidate the long-term consequences, in parallel to the effect of TGR operation.

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