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Nestedness of waterbird assemblages in the subsidence wetlands recently created by underground coal mining

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Abstract

Nestedness has been a research focus in fields of island biogeography and community ecology in recent decades. Although nestedness of faunal assemblages has been investigated in natural wetlands, it remains largely unknown whether and why waterbird communities in artificial wetlands follow nested patterns. We examined the existence of nestedness and underlying drivers in waterbird communities in subsidence wetlands that are recently created by large-scale underground coal mining in the North China Plain. Twelve point-count surveys for waterbirds were undertaken approximately every 2 weeks in 55 subsidence wetlands from September 2016 to April 2017. We used the metric WNODF to estimate nestedness of the assemblages. Partial Spearman rank correlations were performed to examine the association between the nestedness and habitat variables (wetland area, landscape connectivity, wetland age, and habitat diversity) as well as life-history traits (body size, clutch size, dispersal ratio, geographical range size, and migrant status) related to species extinction risk and colonization rate. Waterbird assemblages in the subsidence wetlands were significantly nested. After controlling for other independent variables, the magnitude of nestedness was significantly and negatively correlated with wetland area and species trait linked to extinction risk (i.e., geographical range size). Our results indicate that selective extinction may be the main driver of the nestedness of waterbird assemblages in our study system. However, the nestedness was not due to passive sampling, selective colonization, or habitat diversity. From a conservation viewpoint, both large wetlands and waterbirds with a small geographic range should be protected to maximize the preserved species richness.

Key words: geographical range size, nested pattern, selective extinction, waterbirds, WNODF.

Biotic communities are heterogeneously distributed in space and time, and the pattern of nestedness has been increasingly proposed as an essential metric to measure spatially hierarchical patterns of regional biodiversity (Soininen et al. 2018). Nestedness occurs when species present at relatively depauperate locations constitute subsets of those present at more species-rich locations (Patterson and Atmar 1986). Since its formalization, nested species distributions have been found in a wide range of taxa from bacteria to mammals in various systems (Wright et al. 1998; Schouten et al. 2007; Wang et al. 2010; Soininen and Köngäs 2012; Soininen et al. 2018). Quantifying nested metacommunity structures and understanding the causal drivers shaping the dynamic nature of biodiversity can provide insights into how biodiversity is maintained and help conceive effective management plans (Socolar et al. 2016).

Four main mechanisms have been proposed to explain nested patterns of biotic assemblages, including selective extinction, selective colonization, habitat nestedness, and passive sampling (Cutler 1994). The selective extinction hypothesis predicts that island area will be the main driver of nestedness in systems experiencing species loss or "relaxation" (Wright et al. 1998). This is because species with large minimum area requirement may have greater extinction risk, especially in fragmented habitats, resulting in a predictable sequence of extinction in relation to island size. Selective colonization can also produce nested patterns, where species with greater dispersal ability are more likely to colonize a larger number of sites (Patterson 1987). The habitat nestedness hypothesis ascribes the nestedness of species assemblages to the associated habitat nestedness (Honnay et al. 1999). Nestedness can also be due to passive sampling process because common species are more likely to be observed than rare species in a given habitat (Higgins et al. 2006). As passive sampling does not imply ecological significance, it is suggested that this should be tested prior to other hypotheses (Wright et al. 1998).

Species life-history traits may also provide useful information for assessing the importance of different processes in generating nestedness (Wang et al. 2010, 2012). For example, if dispersal ability is a main driver of nestedness, then functional traits reflecting the relative mobility of species may shape the structure of communities (Frick et al. 2009). In contrast, if selective extinction is the strong determinant of nestedness, life-history traits linked to higher extinction vulnerability might play a major role in structuring species assemblages (Wang et al. 2010, 2012). Despite the links between these species traits and environmental variables (Ulrich et al. 2009), few studies have combined them simultaneously to examine their roles in generating nestedness.

Nestedness of biotic assemblages can be found in almost all habitat patches including forest remnants and wetland systems (Paracuellos and Tellería 2004; Martínez-Morales 2005). Like other habitat islands, wetland networks patchily immersed in surrounding terrestrial landscape matrix perform biologically as real islands and provide an interesting system to study nestedness in a variety of wetland-dependent taxa (De Meester et al. 2005; Soininen et al. 2007; Soininen and Köngäs 2012; Hill et al. 2017). Studies on natural wetlands have found nested metacommunity structures in waterbird assemblages that are highly sensitive to habitat changes, and are often identified as focus of conservation (Paracuellos and Tellería 2004; Sebastián-González et al. 2010). Due to global loss and degradation of natural wetlands, waterbirds increasingly use artificial wetlands in human-dominated landscapes, which has become a widely debated topic in conservation (Navedo et al. 2012; Rajpar and Zakaria 2013). Quantifying nestedness of waterbird communities in artificial wetlands, and exploring the causal underlying drivers may have important implications both in theory and in practice.

Despite increasing interest in waterbird use of various man-made wetlands, little is known about avian assemblages in subsidence wetlands which are mainly created by underground mining (Zhang et al. 2017). During the last 3 decades, massive and continuing underground coal mining in China has created large-scale land subsidence with an annual increase of 7×10^4 ha (Hu et al. 2014). Due to high groundwater levels and abundant rainfall, hundreds of subsidence wetlands, ranging from several hectares to several square kilometers, have been created in the North China Plain (Xie et al. 2013). These man-made wetlands have attracted a wide array of waterbird species to rest, forage, or nest (C. Li, personal

observation), and may provide an effective and interesting habitat island system to test nestedness of biotic communities in fragmented habitats. First, because of relatively small size and clear geographical boundaries, waterbirds in these subsidence wetlands can be readily and thoroughly surveyed. Second, the subsidence wetlands were created in different years, with asynchronous colonization of waterbirds. These man-made wetlands also differ in a wide range of environmental attributes, allowing us to explore effects of habitat heterogeneity on the waterbird metacommunity structures. Finally, these wetlands support both resident and migratory species that differ greatly in habitat requirements, patch occupancy, and other behaviors. Phenology of migratory birds results in highly vagile communities in these wetlands. Investigating hierarchical metacommunity structure of waterbirds in the subsidence wetland network may provide new insights into nestedness theory beyond traditional study systems. In practice, the results may help conceive effective management plans in the less-studied human-dominated landscape.

In this study, we examined the spatially hierarchical distribution pattern of waterbird communities in the subsidence wetlands in the North China Plain. We first tested the hypothesis that waterbird assemblages in these fragmented, man-made, wetlands would follow a nested pattern. In addition, we determined the processes and influencing factors, particularly habitat variables and life-history traits, underlying nestedness of the waterbird assemblages.

Materials and Methods

Study area

The study was carried out in the Huainan–Huaibei coal mining area (3.74×10^6 ha) in Anhui Province, located at the southern part of the North China Plain that encompasses an area of 3×10^7 ha (Figure 1; 32.73°–33.73°N, 116.03°–117.52°E). The region is dominated by flat landscape with a mean elevation of approximately 30 m above sea level. Some low knolls occasionally up to 300 m are located in the northeastern part of the plain. Influenced by typical warm temperate semi-humid monsoon climate, the average annual temperature is 14.7°C, and the average annual rainfall is 970 mm. Most of the precipitation is concentrated in warm seasons between April and August.

The Huainan–Huaibei Plain is one of the 14 largest coal bases in China, which produces 4.17% of the national coal output (Hu et al. 2014). Coal mining in this region began more than 100 years ago and the modern industrialization in recent 3 decades has vastly increased the coal production. Since most of the coals are extracted from underground, land subsidence and submergence have occurred in the coal mining areas. It is estimated that 0.2–0.5 ha of land subsidence will be created by 10,000 tons of raw coal production (Bian et al. 2010). Up to 2010, the massive and continuing coal mining in this region had resulted in more than 3×10^4 ha of subsidence area with an annual expansion of more than 2,000 ha (Xie et al. 2013). Due to the high groundwater level and abundant rainfall in this region, two-thirds of the subsidence land has been flooded, creating hundreds of isolated wetlands scattered on the agricultural matrix. These subsidence wetlands have attracted a large number of resident and migratory waterbirds to rest, forage, and breed (C. Li, personal observation, but also see Supplementary Table S1).

Waterbird surveys

Point counts of waterbirds were carried out in 55 subsidence wetlands with an area of 6,226 ha, accounting for approximately 40%
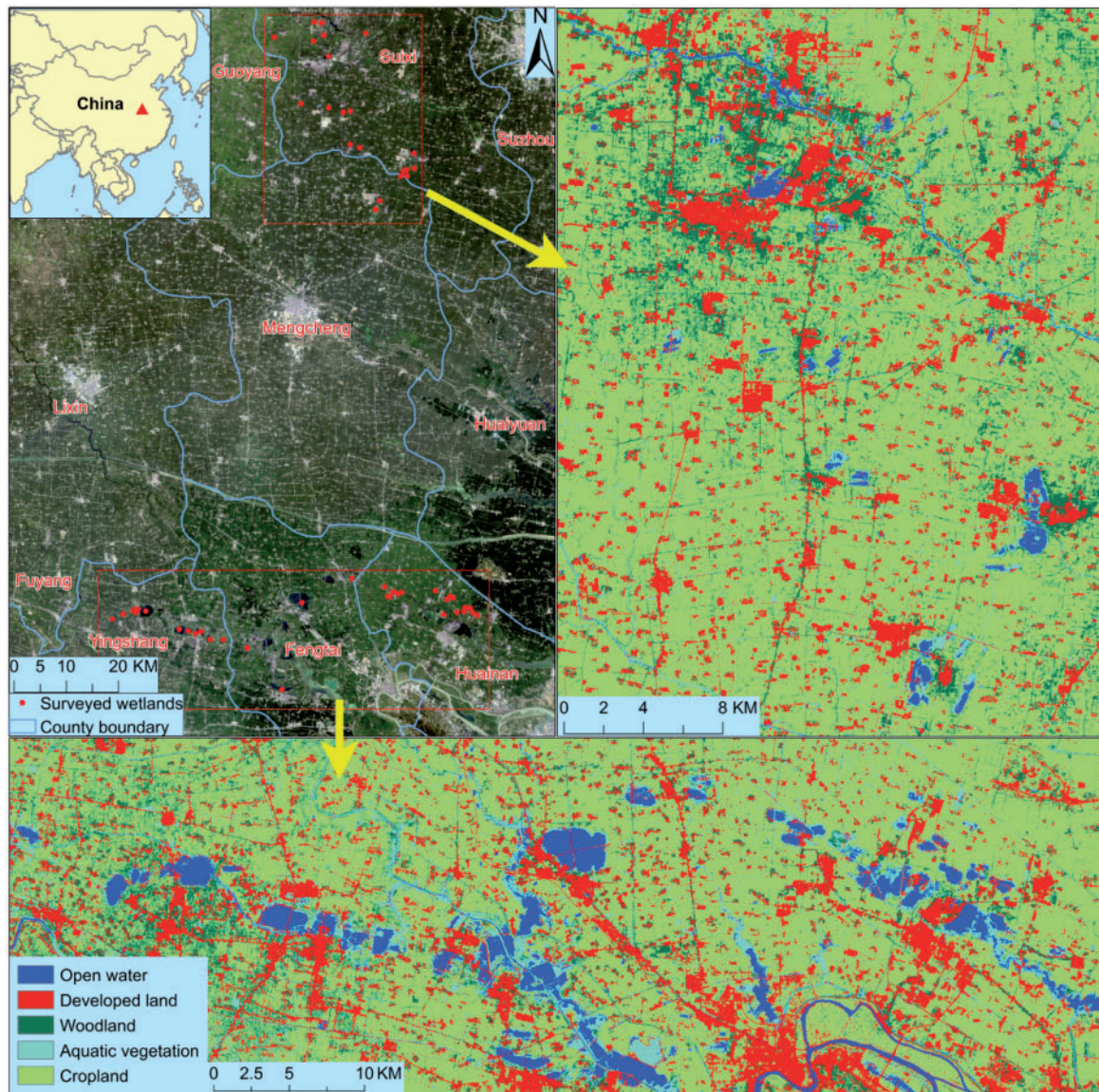
Figure 1. Land-cover and location of the 55 surveyed subsidence wetlands in Huainan–Huaibei coal mining area, China.

of the man-made wetlands in the Huainan–Huaibei coal mining area. These wetlands were selected randomly to represent a wide range of environmental conditions. Depending on the wetland area and accessibility (Cam et al. 2000), we placed 1–6 counting points along its boundary to get an unobstructed view of each sampling wetland. We defined areas within a radius of 1 km at counting points as observation areas that were not overlapped to avoid double counting.

From September 2016 to April 2017, we carried out 12 field surveys approximately every 2 weeks, each covering all the 55 wetlands within 3 clear and calm days. During the field surveys, the "look-see" total counting method (Delany 2005) was employed by the same 2 experienced bird observers to record waterbirds in the selected wetlands. Birds flying over the wetlands were not recorded, except those being flushed out from within the observation areas. Waterbird counting at each point lasted approximately 15 min with the help of binoculars (10 × 42 WB Swarovski) and a telescope (20–60× zoom Swarovski: ATM 80). We defined waterbirds as bird species that are "ecologically dependent upon wetlands" according

to the Ramsar Convention (Gardner and Davidson 2011). They were identified to species level according to the taxonomy by BirdLife International (2016). We classified all the watebird species into 3 groups according to their migration status, namely residents, winter migrants, and summer migrants (Zheng 2011).

Habitat variables

For each subsidence wetland, we selected 4 habitat variables that are commonly considered to influence nestedness, that is, wetland area, landscape connectivity, wetland age, and habitat diversity (Wright et al. 1998; Table 1). The age of a wetland was defined as the time since it was created. This was determined by comparing land-cover changes interpreted by a time series of Landsat images (TM/ETM/OLI) which were acquired every 16 days from 1987 to 2016. To determine the other 3 variables of each subsidence wetland, we first interpreted a remotely sensed image to get a land-cover map of the study area. The image was acquired on 2 September 2016 (Level 1T of Landsat 8 OLI on path 122/row 37) with no cloud cover, and

Table 1. Characteristics of the 55 study subsidence wetlands in the Huainan–Huaibei coal mining area, China

Wetland identity	Area (ha)	Landscape connectivity	Habitat diversity	Wetland age (year)	Species richness	Nestedness rank
N1	7.83	734.66	1.80	4.2	16	31
N2	16.65	756.72	1.54	13.4	15	33
N3	15.75	200.27	1.72	2.1	21	18
N4	51.30	667.83	1.99	13.4	23	13
N5	24.12	696.11	1.42	4.0	13	42
N6	230.94	820.49	1.34	28.0	31	3
N7	105.75	83.52	2.00	2.7	36	2
N8	45.45	214.00	2.00	2.2	23	12
N9	45.72	222.14	1.85	7.1	11	46
N10	70.38	219.37	1.74	6.7	26	7
N11	80.46	267.78	1.94	6.8	18	24
N12	85.32	224.68	1.90	3.6	30	4
N13	245.79	502.91	1.69	17.8	10	47
N14	166.32	520.42	1.39	16.6	22	15
N15	11.79	572.51	2.00	5.8	14	39
N16	20.34	658.55	1.94	6.3	8	50
N17	17.55	664.66	1.14	1.8	25	10
N18	34.29	664.66	1.85	3.5	14	40
N19	103.77	572.93	1.89	7.7	15	32
N20	218.34	663.92	1.69	10.7	8	51
N21	57.24	763.59	1.66	13.4	8	49
S1	106.74	2,187.34	1.43	24.2	24	11
S2	10.26	1,909.49	1.39	6.7	15	38
S3	15.12	1,943.48	1.70	18.8	9	48
S4	15.21	2,470.84	1.84	3.6	16	30
S5	54.09	2,479.19	1.42	14.8	21	19
S6	144.63	2,962.49	1.33	10.4	18	27
S7	84.51	2,942.58	1.56	25.5	26	6
S8	32.40	2,935.28	1.60	8.1	13	45
S9	37.80	2,930.15	1.87	8.5	7	52
S10	88.02	2,950.97	1.58	7.8	19	23
S11	65.88	1,972.41	1.80	6.2	18	26
S12	68.58	1,374.03	1.76	19.7	13	44
S13	31.86	1,287.44	1.41	19.4	18	25
S14	73.62	866.29	1.55	16.1	26	8
S15	66.33	848.49	1.39	14.8	23	14
S16	27.72	846.78	1.43	7.2	20	21
S17	95.40	1,082.90	1.46	3.4	38	1
S18	145.62	816.89	1.97	6.4	19	22
S19	970.38	4,479.91	1.12	8.8	25	9
S20	285.66	4,904.47	1.33	22.6	23	12
S21	136.17	4,506.72	1.32	10.5	16	29
S22	249.93	4,722.83	1.62	5.7	22	16
S23	233.46	2,363.18	1.79	13.7	29	5
S24	113.85	2,728.49	1.38	13.7	20	20
S25	82.80	2,716.35	1.45	14.9	15	37
S26	179.19	2,764.20	1.34	19.3	15	34
S27	296.10	1,922.23	1.13	13.6	22	17
S28	378.27	1,552.49	1.10	9.0	14	41
S29	57.69	1,177.92	1.21	2.5	13	43
S30	24.66	1,175.58	1.24	2.0	6	53
S31	32.94	1,172.60	1.42	2.0	15	36
S32	8.37	1,171.63	1.00	2.0	3	54
S33	139.23	1,226.71	1.61	4.2	17	28
S34	218.16	2,515.21	1.16	6.6	15	35

was downloaded from the USGS website (http://glovis.usgs.gov/). Maximum-likelihood classifier was used in ENVI 5.1 (Exelis VIS Inc.) to identify 5 land-cover categories: cropland, developed land, open water, aquatic vegetation, and woodlands. The overall classification accuracy was 94.4% and the kappa coefficient was 0.91. Wetland area was measured by combining the area of open water and aquatic vegetation within each wetland. To quantify habitat diversity, we used the inverse of Simpson's index: $HD = 1/\sum_{i=1}^{n} p_i^2$, where p_i is the proportion of the total area occupied by the ith of n habitat types (Simpson 1949). We defined landscape connectivity as the total area of wetlands (>1 ha) within a 5-km buffer zone surrounding each wetland. We chose this radius because it may

encompass mean home range size for most waterbird species in this study and thus explain most variation in species richness and abundance (Moilanen and Nieminen 2002; Roach and Griffith 2015). The landscape measure of connectivity is an inverse measure of wetland isolation, that is, wetlands surrounded by a larger percentage of wetlands are less isolated (Diver 2008).

Species life-history traits

We selected 5 commonly cited species traits (body size, clutch size, dispersal ratio, geographical range size, and migrant status) that are linked to species extinction risk and colonization rate in waterbirds. Body size, clutch size, geographical range size, and migrant status are key traits associated with extinction risk (McKinney 1997; Purvis et al. 2000). Dispersal ratio was used as an index of a species' mobility (Wang et al., 2015). We calculated a dispersal ratio (dp) for each species by dividing its mean wing length (mm) by the cube root of its mean mass (g) (Woinarski 1989; Wang et al. 2018). We used body length (mm) to represent body size (Wang et al. 2015). Clutch size was defined as the median number of eggs per nest (Morrow and Pitcher 2003). Following Jones et al. (2003), the geographic range size (km^2) was obtained from published species range maps by digitizing the area into a geographic information system (ArcView 10.2). Migrant status was classified as resident (1), passage migrant (2), winter migrant (3), and summer migrant (4) (Van Turnhout et al. 2010). All the above data were obtained from Zhao (2001) and Zheng (2011). For each of the species traits, if a range instead of the mean was given, we used the arithmetic mean of the limits (Wang et al. 2018).

Data analyses

We used the metric WNODF to quantify nestedness of the waterbird communities (Almeida-Neto and Ulrich 2011). With this metric, nestedness can be calculated not only for the whole incidence matrix (WNODF), but also for species (WNODF$_r$) and sites (WNODF$_c$). We analyzed the abundance metric of waterbird assemblages using the rc null model that maintained the original matrix size and the original abundance in both rows and columns (Almeida-Neto and Ulrich 2011). We then sorted the abundance matrix according to species richness and weights. We used the program NODF* 2.0 (Almeida-Neto and Ulrich 2011) to calculate the above indices and compared them with the results of 1,000 randomly generated communities.

The random placement model (Coleman 1981) was commonly used to test the passive sampling hypothesis (Bolger et al. 1991; Calmé and Desrochers 1999; Wang et al. 2012). We used this model to determine whether the nestedness of the waterbird assemblages could be explained simply by the passive sampling from species abundance distributions (Supplementary Table S1). Under the random placement model, the number of species $S_{(\alpha)}$ to be found in a given region depends on the region's relative area, $\alpha = a_k / \Sigma_{k=1}^{K} a_k$, and the overall abundances n_1, n_2, ... , n_s of the S species represented in C: $S(\alpha) = S - \Sigma_{i=1}^{S}(1 - \alpha)^{n_i}$. The variance σ^2 of $S_{(\alpha)}$ is determined as $\sigma^2(\alpha) = \Sigma_{i=1}^{S}(1 - \alpha)^{n_i} - \Sigma_{i=1}^{S}(1 - \alpha)^{2n_i}$. If more than one-third of the points lie outside one standard deviation (SD) of the expected species–area curve, the random distribution hypothesis should be rejected (Coleman et al. 1982).

The order in which sites and species are sorted by WNODF can be compared with numerous independent variables to evaluate their possible roles in generating nestedness (Patterson and Atmar 2000). To test the effects of wetland characteristics on nestedness, we performed Spearman rank correlations between the wetland ranks in the maximally packed matrix and ranked physical attributes of the wetlands (Table 1). Similarly, to determine the role of species life-history traits in generating nestedness, we calculated Spearman rank correlations between the species ranks in the maximally packed matrix and ranked species traits (body size, clutch size, dispersal ratio, range size, and migrant status; Table 2). Because collinearities occurred among these variables, we computed partial Spearman rank correlations to separate out their independent effects on nestedness (Frick et al. 2009; Wang et al. 2010). Partial Spearman rank correlation analyses were conducted with SAS* 9.2 (SAS Institute, Cary, NC, USA). Statistical significance was set at $P < 0.05$ and data were shown as means ± SD.

Results

Nestedness of waterbird assemblages

The waterbird assemblages in the 55 subsidence wetlands were significantly nested (Table 3). The general nestedness estimator for the whole waterbird-by-wetland abundance matrix (WNODF) exhibited a significantly stronger degree of nestedness than expected (Table 3). Moreover, species composition (WNODF$_c$) and species incidence (WNODF$_r$) were also significantly nested (Table 3).

Determinants of nestedness

The nestedness of waterbird assemblages was in accord with the selective extinction hypothesis (Table 4). After controlling for other independent variables, the nestedness was significantly and negatively correlated with wetland area and species trait linked to extinction risk (i.e., geographical range size) (Table 4).

Nestedness of waterbird assemblages was not consistent with the selective colonization hypothesis (Table 4). Nestedness was not correlated with either landscape connectivity or the dispersal ratio of waterbird species (Table 4).

The nestedness of waterbird assemblages did not appear to result from habitat diversity. After controlling for other independent variables, the nestedness was not correlated with habitat diversity (Table 4).

The nestedness of waterbird assemblages was also not due to passive sampling (Figure 2). None of the observed data points fell within ± 1 SD of the expected species–area curve (Figure 2), which rejected the random placement model.

Discussion

We found that waterbird communities in the subsidence wetlands in the North China Plain were significantly nested. The nestedness of waterbird assemblages in our study system was in accord with the selective extinction hypothesis because species nestedness was significantly correlated with wetland area and species trait linked to extinction risk such as geographical range size. Selective extinction is widely considered as a key driver of nestedness, particularly in fragmented habitats or land-bridge archipelagos that are experiencing species loss or faunal relaxation (Wright et al. 1998; Hill et al. 2011). Species with large minimum area requirement or small geographical distribution range may go extinct first, resulting in a predictable sequence of extinction accordingly (Purvis et al. 2000; Jones et al. 2003). As wetland area was negatively correlated with nestedness, large wetlands deserve more attention at a local scale when conservation investment is limited. In contrast, small wetlands

Table 2. Life-history traits of waterbird species in 55 subsidence wetlands in the Huainan–Huaibei coal mining area, China. Nomenclature follows BirdLife International (2016)

Species	Migrant status	Body size (mm)	Clutch size (*n*)	Dispersal ratio	Geographical range size (km^2)	Nestedness rank
Anser albifrons	3	700.00	4.5	27.96	633.50	53
Fulica atra	3	392.00	9.0	24.86	962.58	8
Egretta garzetta	1	596.50	4.5	35.20	495.09	4
Spatula querquedula	3	368.75	10.0	26.51	962.58	38
Platalea leucorodia	2	818.00	3.5	29.96	962.58	42
Mergellus albellus	3	413.25	8.0	22.59	959.04	30
Aythya nyroca	3	385.25	9.0	21.17	831.97	34
Tringa ochropus	3	234.00	3.5	32.24	962.58	24
Anas poecilorhyncha	1	570.50	9.5	25.92	962.58	11
Ardea cinerea	3	888.00	5.0	38.34	962.58	3
Ardeola bacchus	4	464.25	3.0	34.02	908.64	20
Mareca penelope	3	458.25	8.5	19.36	962.58	44
Tadorna ferruginea	3	594.00	9.0	32.57	959.04	37
Mareca strepera	3	499.50	10.0	27.28	962.58	15
Ardea alba	3	888.25	4.0	36.47	829.40	7
Botaurus stellaris	2	676.75	5.0	32.60	772.69	48
Anser fabalis	3	751.75	5.5	30.04	681.85	26
Podiceps cristatus	3	524.00	4.5	20.09	959.04	5
Vanellus vanellus	2	315.75	4.0	36.34	962.58	36
Aythya fuligula	2	409.75	9.0	22.64	962.58	32
Tringa erythropus	2	293.00	4.0	30.35	962.58	25
Himantopus himantopus	3	353.75	4.0	41.04	962.58	29
Calidris alpina	2	195.50	4.0	29.40	631.37	43
Gavia arctica	2	686.25	1.5	21.23	254.14	59
Gallinula chloropus	1	290.00	8.0	24.28	962.58	2
Zapornia akool	1	265.00	5.0	23.14	217.77	60
Tringa totanus	2	270.00	4.0	30.82	860.71	22
Aythya ferina	2	459.25	8.0	21.02	959.04	31
Larus ridibundus	3	386.75	3.0	45.68	962.58	45
Anser cygnoid	3	850.25	6.0	28.94	800.62	47
Charadrius alexandrinus	3	162.50	4.0	31.08	873.54	28
Ixobrychus sinensis	4	332.50	7.0	28.92	606.69	35
Vanellus cinereus	2	342.00	4.0	35.57	676.36	27
Anser anser	3	807.50	4.5	29.15	962.58	52
Actitis hypoleucos	2	189.25	4.5	29.54	962.58	19
Charadrius dubius	4	168.00	3.5	34.53	962.58	17
Mareca falcata	3	461.25	8.0	27.14	751.21	21
Anas crecca	3	388.50	9.5	26.18	962.58	9
Anas platyrhynchos	3	543.75	9.0	26.78	962.58	10
Bubulcus ibis	4	509.75	6.0	33.99	955.94	23
Spatula clypeata	2	466.25	10.0	28.11	962.58	40
Phalacrocorax carbo	3	798.00	4.0	27.36	962.58	14
Mergus merganser	3	627.50	10.5	24.88	958.93	51
Sterna hirundo	2	341.50	3.0	55.99	881.76	54
Tadorna tadorna	3	570.75	9.0	30.40	959.04	55
Calidris temminckii	2	147.00	4.0	32.91	962.58	49
Tringa nebularia	2	318.75	4.0	31.43	962.58	12
Aythya baeri	2	438.50	7.5	23.03	793.04	33
Gallinago gallinago	2	272.50	4.0	25.08	962.58	18
Hydrophasianus chirurgus	4	445.00	4.0	37.20	292.11	50
Tachybaptus ruficollis	1	258.25	5.5	18.94	962.58	1
Cygnus columbianus	3	1,165.50	3.5	28.30	659.93	39
Zapornia pusilla	2	174.25	7.5	24.64	838.82	56
Chlidonias hybrida	4	251.50	3.0	49.62	824.74	13
Nycticorax nycticorax	4	525.00	4.0	32.94	842.36	16
Larus argentatus	3	614.50	2.5	43.55	438.37	46
Aix galericulata	3	429.75	9.5	26.75	606.69	57
Charadrius placidus	2	210.75	3.5	34.05	796.58	58
Anas acuta	2	567.50	8.5	28.25	962.58	41
Ardea intermedia	4	666.50	4.0	39.68	492.24	6

will have less conservation value because they have a large degree of overlap in species composition with large wetlands (Supplementary Table S1). In addition, by assessing the risk of local extinction in waterbird species with different life histories, management strategies designed to prevent their future extinction can be implemented more effectively (Wang et al. 2010, 2012; Soga and Koike 2013). As species with small geographical distribution range are more vulnerable to extinction (Purvis et al. 2000; Jones et al. 2003), these waterbird species need prior conservation.

The selective colonization hypothesis could not explain the nestedness in our study system because species nestedness was not correlated with landscape connectivity or species dispersal ratio. Three main factors may explain why this correlation is weak. First, the isolation of subsidence wetlands may not effectively prevent the dispersal of waterbirds with high mobility among wetlands in our study system (Figure 1). In addition, the stepping stone effect of some small wetlands may dilute the effect of isolation by distance (Soga and Koike 2013; Pérez-Hernández et al. 2014). Finally, the biologically meaningful quantification of isolation is notoriously difficult (Lomolion 1996; Bergerot et al. 2012), which may preclude strong inference about selective colonization on nestedness.

The nestedness of waterbird assemblages was not attributable to habitat diversity. Habitat nestedness is considered as the most parsimonious process to explain species nestedness because it points directly to associations between species and their habitats (Calmé and Desrochers 1999). Up to now, few studies have explicitly examined the relationship between habitat nestedness and species nestedness. Our results are inconsistent with several previous studies (e.g., Calmé and Desrochers 1999; Schouten et al. 2007; Wang et al. 2012). The weak correlation between waterbird nestedness and habitat diversity is probably due to the little variation in habitat diversity (Table 1). Due to intense human activities, the subsidence wetlands were dominated by open water and some aquatic vegetation. We could not identify other habitat types, such as mudflats and

riparian grassland. Further studies may consider identifying water areas at different water depths which may provide habitats for different species.

The nestedness of waterbird assemblages in the subsidence wetlands was also not resulted from passive sampling. Nestedness is hypothesized to arise from random samples of species differing in their relative abundances (Andrén 1994; Cutler 1994; Higgins et al. 2006). However, passive sampling played little role in the development of waterbird nestedness in our study system because the random placement model was rejected. Although some ecologists emphasize that the passive sampling hypothesis should be tested prior to other hypotheses (Andrén 1994; Cutler 1994), the sampling effect has rarely been examined probably because of the difficulty involved in collecting abundance data (Wright et al. 1998). Our study provides further test for the passive sampling hypothesis (Wang et al. 2010, 2012; Xu et al. 2017).

Two potential caveats may exist in our study. First, our study cannot completely distinguish selective extinction mediated through area effects from the target effect. The target effect indicates that colonization rates may also increase with habitat area because larger islands are easier to be found (Russell et al. 2006). To test the target effect, multi-year survey data are required to calculate the colonization rate and extinction rate (Russell et al. 2006). As waterbirds in the studied wetlands are surveyed only in 1 year, the target effect cannot be tested in our study. Long-term monitoring is thus needed to confirm that target effects are not muddling our results. In addition, the difference in detection probabilities among waterbird species (McKinney 1997; Cam et al. 2000) may confound our estimates of abundance, which in turn may bias our test of the passive sampling hypothesis. In our case, the abundance of some rare species was low (Supplementary Table S1), suggesting that our estimate of waterbird abundance may be biased. Investigating to what extent

Table 3. Results of nestedness analyses using the program NODF conducted on the species-by-sites abundance matrix of waterbird assemblages in the 55 subsidence wetlands in Huainan–Huaibei coal mining area, China

Nestedness metric	$WNODF_{obs}$	$WNODF_{exp}$	P-values
WNODF	41.12	73.93±1.32	<0.001
$WNODF_c$	45.49	75.38±1.00	<0.001
$WNODF_r$	37.45	72.75±1.97	<0.001

Notes: Given are observed WNODF ($WNODF_{obs}$), expected WNODF ($WNODF_{exp}$), and Monte Carlo-derived probabilities that the matrix was randomly generated 1,000 permutations. WNODF, general nestedness estimator for the whole abundance matrix; $WNODF_c$, column nestedness estimator among sites (species composition); $WNODF_r$, row nestedness estimator among species (species incidence).
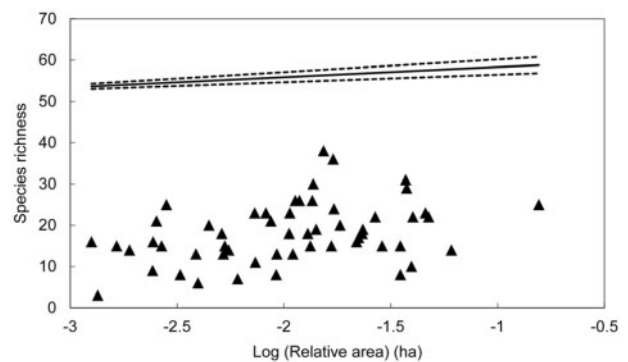

Figure 2. Comparison of observed data to expected values under the random placement model for waterbirds in subsidence wetlands in the Huainan–Huaibei coal mining area, China. Expected values (solid line) and associated standard deviations (±1 SD; dashed line) are shown. Filled triangles represent observed species richness.

Table 4. Relationships between rank orders of sites and species in the maximally nested matrix and orders of sites and species after rearranging the matrix according to each explanatory variable

Habitat variables				Species life-history traits				
Wetland area (ha)	Landscape connectivity	Habitat diversity	Wetland age	Migrant status	Body size (mm)	Clutch size (n)	Dispersal ratio	Geographical range size (km²)
−0.423**	0.093	−0.132	0.341	−0.134	−0.020	0.010	−0.018	−0.355**

Notes: Values are partial Spearman rank correlations. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

the observed abundance may differ from the true abundance of waterbirds needs more detailed surveys and warrants further evaluation.

Ethical note

No cruelty occurred to animals in this study because we only observed birds in the field with the help of binoculars and a telescope.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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