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Nestedness and underlying processes of bird assemblages in Nanjing urban parks

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Abstract

Nestedness is an important pattern frequently reported for species assemblages on islands or fragmented systems. However, to date, there are few studies that comprehensively investigated faunal nestedness and underlying processes in urbanized landscapes. In this study, we examined the nestedness of bird assemblages and its underlying causal mechanisms in 37 urban parks in Nanjing, China. We used the line-transect method to survey birds from April 2019 to January 2020. We used the Weighted Nestedness metric based on Overlap and Decreasing Fill (WNODF) to estimate the nestedness of bird assemblages. We applied spearman partial correlation test to examine the relationships between nestedness ranks of sites and park characteristics (area, isolation, anthropogenic noise, number of habitat types, and building index), as well as between nestedness ranks of species and their ecological traits (body size, geographic range size, clutch size, minimum area requirement, dispersal ratio, and habitat specificity). We found that bird assemblages in urban parks were significantly nested. Park area, habitat diversity, building index, habitat specificity, and minimum area requirement of birds were significantly correlated with nestedness. Therefore, the nestedness of bird assemblages was caused by selective extinction, habitat nestedness, and urbanization. However, the nestedness of bird assemblages did not result from passive sampling, selective colonization, or human disturbance. Overall, to maximize the number of species preserved in our system, conservation priority should be given to parks with large area, rich habitat diversity, and less building index. From a species perspective, we should focus on species with large area requirement and high habitat specificity for their effective conservation.

Key words: birds, building index, habitat nestedness, habitat specificity, minimum area requirement, selective extinction, urbanization

Urbanization is the process that natural landscape changes to land with specific uses due to human intervention (Sahani and Raghavaswamy 2018). With the rapid worldwide development of urbanization, the structure and communities of previous natural ecosystems have been changed fundamentally (Green and Baker 2003). Specifically, urbanization often fragmented the once continuous forest into many small woodlots or urban parks that are isolated from each other by an inhospitable urban matrix (Soulé et al. 1988). In this context, parks in urban areas often act as "islands" or habitat fragments for wildlife (Fernández-Juricic and Jokimäki 2001). The isolation of urban parks has profound influences on wildlife biodiversity and often leads to the decline or even extinction of vulnerable species (Bolger et al. 1991; Crooks et al. 2001). However, the community composition pattern, such as nestedness, has rarely been investigated in urbanized landscapes.

Nestedness, or nested species subset, is a common pattern frequently reported for faunal assemblages on islands or fragmented systems (Wright et al. 1998; Watling and Donnelly 2006).

Nestedness occurs when species present at relatively species-poor locations constitute proper subsets of those present at more species-rich locations (Darlington 1957). However, nestedness studies only became prevalent after Patterson and Atmar (1986) proposed the first community-wide metric to measure nestedness statistically (Whittaker and Fernández-Palacios 2007; Wang et al. 2012). At present, nestedness has become an important research field in island biogeography and conservation biology (Patterson 1987; Ganzhorn and Eisenbeiß 2001; Fleishman et al. 2007; Whittaker and Fernández-Palacios 2007).

A variety of hypotheses have been proposed to interpret nestedness, including passive sampling, selective extinction, selective colonization, habitat nestedness, and human disturbance (Cutler 1994; Cook and Quinn 1995; Wright et al. 1998; Fernández-Juricic 2002). Passive sampling could generate nestedness because rare species have less chance to be sampled in a given area than the common species (Andrén 1994; Cutler 1994; Higgins et al. 2006). The selective extinction hypothesis predicts that area is a main driver of nestedness because species with large area requirements have greater extinction risk (Wright et al. 1998). According to the selective colonization hypothesis, habitat isolation would create nestedness through dispersal limitation as species differ in their ability to colonize distant sites (Darlington 1957). The habitat nestedness hypothesis posits that the nestedness of species assemblages is due to their reliance on habitats that have a nested distribution (Calmé and Desrochers 1999; Honnay et al. 1999). Finally, human disturbance can also promote nestedness because species have different tolerance to disturbance in human dominated landscapes (Fernández-Juricic 2002; González-Oreja et al. 2012).

Besides habitat characteristics, species life-history or ecological traits may also have important influences on nestedness (Schouten et al. 2007; Meyer and Kalko 2008; Frick et al. 2009). For instance, ecological traits related to the colonization capacity and extinction risk of butterflies are found to affect nestedness (Dennis et al. 2012; Xu et al. 2017). If extinction susceptibility is the main cause of nestedness, species life-history traits associated with extinction proneness will structure composition patterns (Schouten et al. 2007; Wang et al. 2010; Xu et al. 2017). On the contrary, if dispersal ability is the primary determinant of nestedness, ecological characteristics reflecting the dispersal ability of species may order species occurrence patterns (Meyer and Kalko 2008; Dennis et al. 2012).

Nanjing is located in the economic zone of the Yangtze River Delta and has been experiencing rapid urbanization in the past 50 years (Yuan et al. 2018). In 1949, the total population of Nanjing was just 2.027 million, of which non-agricultural population was 0.983 million. In 2018, however, the registered population of Nanjing increased rapidly to 6.969 million, including the 5.012 millions of non-agricultural population (Nanjing Statistics Bureau 2019). Meanwhile, the length of paved roads in Nanjing has increased from 1,802 km at the beginning of this century to 8,469 km in 2018. There are 140 urban parks in Nanjing by 2018 with a total area of 7,243 ha (Nanjing Statistics Bureau 2019). The rapid rate of urbanization of Nanjing may have serious impacts on bird community composition. However, to date, very few studies have investigated the nestedness of bird assemblages in Chinese cities.

In this study, we examined the nested distribution of bird assemblages on 37 urban parks in Nanjing, China. Our study has 3 main objectives as follows: 1) to evaluate whether bird assemblages in Nanjing urban parks conforms to the nested subset pattern; 2) to determine the causal mechanisms underlying the nestedness of bird assemblages; and 3) to apply the nestedness theory to direct urban park planning and protect bird diversity in our system.

Materials and Methods

Study area

Nanjing (31°14′–32°37′N, 118°22′–119°14′E) is the capital of Jiangsu province and one of the most urbanized cities in China. It lies in the middle and lower reaches of the Yangtze River, crossing the 2 banks of Yangtze River (Figure 1). There are 6,658.02 km^2 of administrative area in Nanjing, with 11 municipal jurisdictions and 8.346 million permanent population. Nanjing has a subtropical monsoon climate with 4 distinct seasons. The average annual temperature of Nanjing was 17.0°C, and the annual precipitation was 1,267.1 mm. The forest coverage rate of Nanjing is 25.42%, and the urban green coverage rate is 45.06%.

We selected a total of 37 urban parks (Figure 1) as study sites. Most of the parks are distributed in several administrative districts with high level of urbanization (Figure 1). These parks were selected to exhibit gradient changes in the landscape variables, including park area, isolation, habitat type, building index, and human disturbance (Yang et al. 2020). For example, the area of parks ranged from 2.20 to 514.68 ha, the isolation from the species pool ranged from 19.50 to 1,4341.71 m, and the number of habitat types varied from 2 to 12 (Table 1).

Sampling methods

Bird surveys

We used the line-transect method (Bibby et al. 2000) to survey birds in the 37 urban parks. We roughly arranged the number of transects relying on the size of the study park (Fernández-Juricic and Jokimäki 2001; Wang et al. 2013). Accordingly, 8 transects were sampled in park 1 (the largest park, area = 514.68 ha), 4 transects in parks 2–7 (60 < area <500 ha), 2 transects in parks 8–24 (10< area <60 ha), and 1 transect in parks 25–37 (area <10 ha) (Table 1).

The survey of birds was conducted from April 2019 to January 2020. We usually surveyed birds at 0.5 h after sunrise to 11:00 AM and from 3:00 PM to 0.5 h before sunset. During the survey, 2 investigators observed birds with the CELESTRON Outland X 10 × 24 binoculars along the transects at a speed of about 2.0 km/h. The length of each transect was not fixed, but flexible to run through the park to make a thorough search for all species (Fernández-Juricic 2002). We recorded all bird species seen or heard within 50 m of the transects, except for birds passing by (Wang et al. 2010). Bird survey was not conducted in bad weathers, such as heavy rain, strong wind, or high temperature (Robbins 1981). Each park was surveyed once a month and 10 times in total. To reduce system errors, the order and walking routes of the parks were random and rotated for each survey (Wang et al. 2010).

The species accumulation curve is widely used to judge the sampling adequacy and estimate the true species richness (Colwell et al. 2004; Wang et al. 2012; Xu et al. 2017). Therefore, we evaluated bird inventory completeness for each park with randomized sample-based species accumulation curve (Colwell et al. 2004). The extrapolated bird species richness of each park was calculated using the common nonparametric estimator Chao 1 (Colwell et al. 2004). The analyses were performed using the "vegan" package (Oksanen et al. 2019) in R version 4.0.0 (R Core Team 2020).

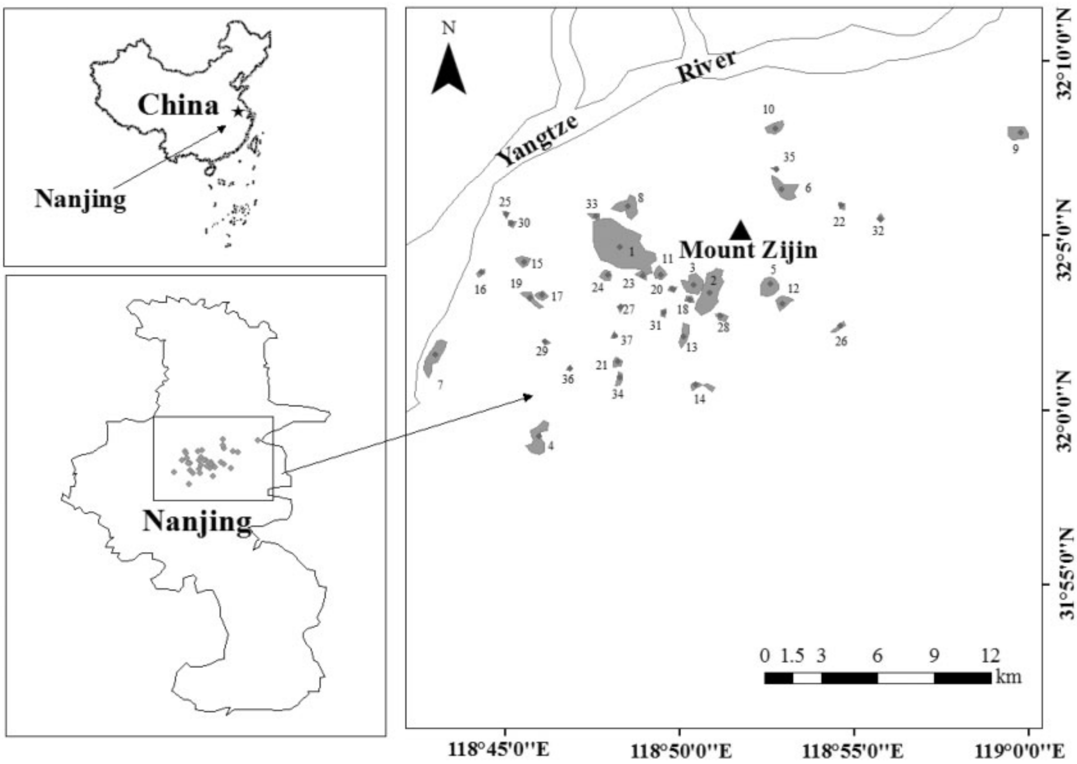

Figure 1. The location of 37 urban parks in Nanjing, China. See Table 1 for park code and names.

Habitat variable surveys

For each park, we selected 5 habitat variables that were commonly considered to influence species nestedness (Table 1): area, isolation, number of habitat types, anthropogenic noise, and building index (Wright et al. 1998; Wang et al. 2004; González-Oreja et al. 2012). The area, isolation, and building index of the parks were all measured with Google Earth and the geographic information system (GIS) (ArcView 10.2). Isolation1 was measured as the distance from the park to the Zijin Mountain (Zhongshan National Park), and Isolation2 was the distance from the park to the nearest larger park, both of which reflect the potential source of species for the smaller park (Fernández-Juricic 2002; Wang et al. 2013). We regarded the Zijin Mountain as a regional species pool because it is the largest forest park in Nanjing region and it has not been fragmented with high forest coverage (Zhang et al. 2018). The building index is considered as the level of urbanization where the park is located (Bolger et al. 1997; Wang et al. 2009). After Bolger et al. (1997), the building index was constructed by first measuring the proportions of area covered by buildings around each park at radii of 250, 500, 1,000, and 2,000 m in a GIS (ArcView 10.2). Afterward, the proportion in the 250 m circle was given a weight of 1.0, the proportion in the 500 m buffer a weight of 0.5, 1,000 m a weight of 0.25, and 2,000 m a weight of 0.125. The weighted proportions were then summed to form the building index (Bolger et al. 1997). We surveyed and divided all the habitats in urban parks into 12 types (Table 2): broadleaf woodland, coniferous woodland, coniferous/broad-leaf mixed woodland, dense shrub, sparse shrub, short trees, medium high trees, high trees, water area, clearing, hill, and building (Wang et al. 2013). We used the Aicevoos K8 noise meter to measure park noise, which was considered as a level of human interference (González-Oreja et al. 2012). During each survey, 3–5 points in the park were selected to measure the noise level according to the size of the park. The maximum and minimum noise levels within 1 min were recorded at each point, and the arithmetic mean of noise level in each park was calculated (Wang et al. 2013).

Species ecological traits

We collected data on 6 life-history and ecological traits associated with bird extinction risk and colonization rate as follows: body size, geographic range size, clutch size, minimum area requirement, dispersal ratio, and habitat specificity (Table 3). We used body length to represent body size (Wang et al. 2010). The median number of eggs per nest was used as clutch size (Wang et al. 2015). Based on the most recent distribution range maps for all 1,445 Chinese birds (Zheng 2017), the geographic range size within China was obtained by digitizing the area into a GIS (ArcView 10.2) (Wang et al. 2018). We calculated the dispersal ratio (dp) for each species by dividing its mean wing length (mm) by the cube root of its mean mass (g), representing the mobility ability of species (Wang et al. 2018). The minimum area requirement is defined as the minimum park area occupied by each species (Davidar et al. 2002; Wang et al. 2010; Xu et al. 2017). Habitat specificity is measured as the number of habitat types occupied by a species in the park (Wang et al. 2013, 2018).

Statistical analyses

Quantification of nestedness

We used the nestedness metrics Nestedness metric based on Overlap and Decreasing Fill (NODF) and WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill) to estimate the nestedness of bird assemblages (Ulrich 2010; Almeida-Neto and Ulrich 2011). WNODF is a simple modification of NODF. The most advantage of WNODF over other metrics is that it can use species abundance rather than just richness to quantitatively estimate the

Table 1. Characteristics of the 37 study parks in Nanjing, China

Park code	Park name	Park area (ha)	Noise (dBA)	Isolation1 (m)	Isolation2 (m)	Building index	Number of habitat types (*n*)	Observed richness (*n*)	Expected richness Chao1(SE)[a]	Survey completeness	Nested matrix rank
1	Xuanwuhu	514.68	56.3 ± 6.7	5,226.65	5,226.65	101.57	11	41	21.2(1.84)	0.94	4
2	Mingxiaoling	160.49	57.6 ± 1.7	1,892.79	2,324.98	35.11	11	44	25.0(7.24)	0.76	2
3	Botanical garden	100.64	56.1 ± 3.1	2,247.10	1,122.29	37.92	11	36	39.2(6.43)	0.82	6
4	Juhuatai	98.54	59.0 ± 4.3	12,458.44	7,922.71	158.59	4	20	28.0(5.52)	0.82	27
5	Linggu temple	63.66	60.8 ± 3.5	1,461.35	346.25	15.89	8	32	25.5(3.15)	0.90	9
6	Jubaoshan	62.39	56.6 ± 4.4	4,566.55	3,977.97	75.90	12	44	35.0(7.10)	0.80	3
7	Green expo garden	61.38	53.9 ± 2.0	1,4411.35	8,215.56	65.62	10	38	32.0(7.10)	0.78	5
8	Hongshan zoo	52.51	58.5 ± 6.0	5,834.04	522.35	139.55	7	21	36.0(13.69)	0.58	25
9	Xianlinhu	45.33	56.1 ± 3.5	14,341.71	3,229.51	61.44	7	32	32.6(5.34)	0.83	8
10	Taipingshan	33.55	56.6 ± 1.5	7,598.04	2,252.73	133.41	6	26	20.5(1.29)	0.98	15
11	Baima	33.33	59.5 ± 1.7	3,581.93	69.42	86.36	9	32	59.6(11.64)	0.74	7
12	Zhongshan sports park	29.85	55.8 ± 4.6	2,527.57	335.05	87.31	8	28	34.5(3.16)	0.93	12
13	Yueyahu	29.60	58.6 ± 7.1	4,537.64	665.75	209.04	6	27	41.8(4.20)	0.91	13
14	Qiqiaoweng wetland park	29.25	59.4 ± 1.2	6,403.02	1,784.88	64.90	10	46	17.0(1.81)	0.94	1
15	Gulin	21.04	57.0 ± 5.2	9,594.12	2,946.17	199.41	11	28	49.0(4.31)	0.90	11
16	Zhenghe treasure ship ruins park	18.67	52.1 ± 3.8	11,520.18	1,409.22	126.90	5	23	23.0(0.16)	1.00	21
17	Qingliangshan	18.33	58.2 ± 1.8	8,944.65	1,545.59	185.93	4	17	26.0(4.15)	0.88	31
18	Qianhu	17.78	58.3 ± 4.4	2,783.20	19.50	83.22	5	25	33.2(4.33)	0.87	17
19	Stone city	16.94	57.7 ± 1.5	9,522.38	74.49	180.13	4	25	53.0(6.65)	0.87	18
20	Pipa lake	16.58	55.0 ± 4.3	3,060.95	285.73	93.16	6	29	27.0(2.88)	0.93	10
21	Bailuzhou	15.93	56.5 ± 6.0	7,523.61	2,730.40	201.50	5	19	17.0(0.00)	1.00	29
22	Guishan	14.82	60.1 ± 3.1	5,586.74	1,668.50	164.90	8	25	18.5(1.02)	0.97	16
23	Jiuhuashan	12.95	56.2 ± 5.3	4,509.45	43.45	124.47	7	27	27.0(2.58)	0.93	14
24	Beijige	11.95	56.4 ± 6.1	5,957.47	304.18	156.90	4	23	26.3(0.92)	0.99	24
25	Hydrangea	9.56	53.1 ± 1.7	10,653.16	2,105.76	182.10	5	16	21.3(0.73)	0.99	33
26	Nanwanying	9.35	60.7 ± 3.0	5,227.85	2,359.27	126.56	6	23	25.5(3.15)	0.90	22
27	Nanjing presidential palace	9.30	54.4 ± 2.8	5,797.99	1,398.77	218.80	5	15	46.0(13.18)	0.70	36
28	Xiamafang	9.18	52.0 ± 3.1	2,738.44	422.54	125.47	10	23	30.0(7.27)	0.80	23
29	Nanhu	9.10	60.3 ± 5.9	9,513.70	2074.84	206.11	5	23	22.0(7.22)	0.73	20
30	Bazishan	8.50	59.4 ± 3.5	10,380.34	94.31	194.12	4	20	43.6(2.83)	0.94	28
31	Nanjing Forbidden City	5.28	61.0 ± 3.0	4,205.25	858.19	184.37	5	16	16.0(2.29)	0.94	34
32	Xiaohong stone carving park	4.76	56.8 ± 1.9	6,776.72	1,393.01	115.63	5	24	17.8(1.42)	0.96	19
33	Shencemen	4.60	59.9 ± 3.9	6,972.32	253.50	179.49	5	18	30.8(4.20)	0.88	30
34	Wudingmen	4.40	63.7 ± 4.0	8,026.49	192.68	184.65	5	21	9.0(0.24)	1.00	26
35	Yaohuamen	3.54	54.7 ± 2.6	5,474.09	185.67	104.82	2	15	45.3(8.85)	0.79	35
36	Yuyuan	3.51	57.4 ± 1.7	9,230.13	1,207.27	189.86	6	17	30.0(2.58)	0.93	32
37	Zhenghe	2.20	62.4 ± 4.6	6,693.59	1,172.90	222.68	4	9	15.0(0.24)	1.00	37

Isolation1 is given as distance to the Zijin Mountain and Isolation2 is given as distance to the nearest larger park. , [a]Chao1 is the nonparametric estimator of species richness.

Table 2. Habitat types and their descriptions in 37 study parks in Nanjing, China

Habitat type	Description
Broad-leaf woodland	Broad-leaf tree >50%
Coniferous woodland	Coniferous tree >50%
Mixed woodland	Broad-leaf and coniferous trees mixed, both <50%
High trees	Trees >5 m in height
Medium high trees	Trees >2.5 m, but <5 m in height
Short trees	Trees <2.5 m in height
Dense shrub	Hard to walk in, shrubs with intervals <10 cm
Sparse shrub	Easy to walk in, shrubs with intervals >30 cm
Water area	Including shallow water area, ponds or streams
Cleaning	Including bare ground and grassland
Hill	High land >50 m in height
Building	Human construction such as houses and pavilions

degree of nestedness (Wang et al. 2013). WNODF can estimate the nestedness of the matrix by analyzing species (WNODFr) and sites (WNODFc) separately. We used the rc null model provided by WNODF to maintain the species richness and abundance of the original matrix rows and columns. It randomly generated 1,000 matrices and estimated the statistical results within the 95% confidence interval. All the above calculations were performed using the program NODF version 2.0 (Almeida-Neto and Ulrich 2011).

Determinants of nestedness

We used the random placement model to determine whether the nestedness of bird assemblages in urban parks (Supplementary Appendix 1) was caused by passive sampling (Higgins et al. 2006; Wang et al. 2010). The random placement model (Coleman 1981) predicts that the expected species richness ($S_{(\alpha)}$) depends on the relative area, $\alpha = a_k / \sum_{k=1}^{k} a_k$, and the abundance ($n_i$) of each species in the region, $S_{(\alpha)} = S - \sum_{i=1}^{s} (1-\alpha)^{ni}$. In the above model, a_k is the observed area of a certain location and S is the sum of the species richness at all locations. $\sigma_{(\alpha)}{}^2$ is the standard deviation of $S_{(\alpha)}$ and is calculated as $\sigma_{(\alpha)}{}^2 = \sum_{i=1}^{s} (1-\alpha)^{ni} - \sum_{i=1}^{s} (1-\alpha)2^{ni}$. If more than 1/3 of the observed values are not within 1 standard deviation (SD) of the prediction curve, the passive sampling hypothesis will be rejected (Coleman 1982).

Using the program NODF version 2.0 (Almeida-Neto and Ulrich 2011), we also estimated whether the habitat-by-site matrix (Supplementary Appendix 2) is nested. If the habitat-by-site matrix is significantly nested, then the habitat nestedness hypothesis is supported and can explain the nested distribution of bird assemblages in our system (Calmé and Desrochers 1999; Wang et al. 2013).

After rearranging the species-by-site matrix using the program NODF, a maximally ranked matrix could be obtained (Supplementary Appendix 1). To determine which habitat variables would influence nestedness, we calculated Spearman rank correlations between the park ranks in the maximally packed matrix and ranked physical attributes of parks (area, isolation, number of habitat types, anthropogenic noise, and building index) (Table 1) (Patterson and Atmar 2000). Similarly, to evaluate which species traits would affect nestedness, we conducted Spearman rank correlations between the species ranks in the maximally packed matrix and ranked species ecological traits (Table 3) (Meyer and Kalko 2008; Wang et al. 2010). We used Spearman partial correlation analysis to avoid the problem of collinearities among the variables (Supplementary Appendices 3 and 4) (Frick et al. 2009; Shipley 2000). The above analyses were performed using the ppcor package in R version 4.0.0 (R Core Team 2020).

Results

General sampling results

A total of 76 bird species belonging to 13 orders were observed during the study period in the 37 study parks (Table 3; Supplementary Appendix 1). The majority of species were common in the study region and China. However, *Parus venustulus*, *Aegithalos caudatus*, and *Turdus mandarinus* were 3 endemic species of China (Supplementary Appendix 1). Moreover, *Milvus migrans* and *Buteo buteo* were listed as Chinese second class protected birds.

The observed species richness in each park varied from 9 to 46 (Table 1). According to the expected true species richness, the survey completeness for the 37 parks was very high, ranging from 73% to 100% (Table 1). Moreover, the species accumulation curve approached an asymptote (Figure 2), indicating a high level of bird inventory completeness for all the 37 parks.

Nestedness of bird assemblages

The whole species-by-site matrix for bird assemblages in Nanjing urban parks was significantly nested whether using the nestedness metric of WNODF or NODF (Table 4). In addition, species composition and species incidence were also significantly nested (Table 4).

Mechanisms determining nestedness

The nestedness of bird assemblages in Nanjing urban parks was consistent with the selective extinction hypothesis (Tables 5 and 6). Spearman partial correlation analyses revealed that nestedness was significantly correlated with park area (Table 5) and species ecological traits linked to extinction risk (minimum area requirement and habitat specificity) (Table 6).

The nestedness of bird assemblages in Nanjing urban parks could be attribute to the habitat nestedness hypothesis (Table 4). We found that the habitat-by-site matrix (Supplementary Appendix 2) in Nanjing urban parks was significantly nested (Table 4). Species nestedness was also significantly and negatively correlated with habitat diversity after controlling for other independent variables (Table 5), further verifying the habitat nestedness hypothesis.

The level of urbanization also influenced the nestedness of bird assemblages in Nanjing urban parks. Spearman partial correlation analyses suggested that the nestedness of bird assemblages was significantly and positively correlated with building index as a measure of the level of urbanization (Table 5).

However, the nestedness of bird assemblages in Nanjing urban parks was not in accord with the human disturbance hypothesis (Table 5). We found that anthropogenic noise had no significant effect on nestedness after controlling for other independent variables (Table 5).

The random placement model showed that the nestedness of bird assemblages in Nanjing urban parks was not due to passive sampling (Figure 3). Only 1 point of the observed bird richness was

Table 3. Life-history and ecological traits of bird species in 37 urban parks in Nanjing, China

Species	Body length (mm)	Geographic range size (km^2)	Clutch size (*n*)	Minimum area requirement (ha)	Dispersal ratio (db)	Habitat specificity (*n*)	Number of parks occupied (*n*)	Nested matrix rank
Zosterops japonicus	103.15	532.01	3.00	11.95	12.18	4	9	36
Acridotheres cristatellus	121.15	351.76	2.50	3.51	16.87	5	21	19
Fulica atra	391.00	961.58	9.00	45.33	12.86	1	1	65
Motacilla alba	175.75	961.58	5.50	3.51	31.76	2	24	15
Egretta garzetta	596.50	295.09	2.50	4.40	35.10	1	20	20
Ficedula zanthopygia	111.15	669.71	5.50	29.25	30.36	4	4	51
Pycnonotus sinensis	186.75	285.38	2.00	2.20	16.78	11	37	1
Lonchura striata	111.50	211.58	5.00	4.60	11.35	3	4	48
Turdus eunomus	120.00	838.81	2.00	29.25	30.65	1	1	64
Picumnus innominatus	101.50	276.25	3.50	16.94	12.15	1	1	75
Ceryle rudis	178.00	192.13	2.50	45.33	18.88	1	1	72
Anas zonorhyncha	570.50	961.58	9.50	45.33	15.91	1	1	63
Phoenicurus auroreus	121.75	796.58	6.50	3.51	17.67	7	17	24
Ardeola bacchus	262.15	908.62	3.00	12.95	32.01	1	9	39
Dendrocopos major	119.50	851.97	5.00	9.35	31.01	5	9	37
Cuculus canorus	310.15	961.27	1.00	14.82	23.16	3	3	56
Parus cinereus	132.15	925.88	7.50	3.51	17.79	9	34	8
Upupa epops	180.75	961.58	7.00	33.33	35.89	1	1	74
Hypsipetes leucocephalus	120.00	211.58	3.00	11.95	31.60	3	5	47
Dicrurus macrocercus	165.75	716.91	3.50	14.82	38.01	3	5	46
Garrulax perspicillatus	192.75	310.86	2.00	2.20	12.77	8	36	4
Gracupica nigricollis	182.00	187.05	5.00	29.25	19.35	4	2	58
Garrulax pectoralis	197.50	317.19	2.00	9.18	15.11	1	5	44
Gallinula chloropus	190.00	961.58	8.00	3.51	12.18	1	17	22
Eophona personata	113.50	596.51	3.50	3.54	16.51	3	9	35
Eophona migratoria	188.50	596.51	2.50	3.54	17.67	5	22	18
Pycnonotus jocosus	193.15	181.95	3.00	100.64	17.01	1	1	67
Amaurornis akool	165.00	117.77	5.00	29.25	13.12	1	1	68
Aegithalos concinnus	100.75	262.20	6.50	2.20	15.91	8	27	13
Tarsiger cyanurus	136.00	961.58	5.50	11.95	31.60	6	9	38
Urocissa erythrorhyncha	580.75	535.82	2.50	9.18	32.17	7	12	30
Zoothera aurea	182.50	961.58	2.50	33.33	30.81	1	2	62
Garrulax canorus	113.50	323.27	2.00	8.50	13.05	3	8	42
Pardaliparus venustulus	96.00	238.15	6.00	11.95	17.81	6	10	32
Phylloscopus inornatus	97.75	796.58	5.50	5.28	17.97	4	16	26
Emberiza chrysophrys	150.00	393.82	2.00	61.38	18.30	1	1	66
Phylloscopus proregulus	92.15	821.36	5.50	4.40	18.01	4	17	23
Turdus hortulorum	115.00	766.05	2.00	8.50	19.27	3	7	43
Motacilla cinerea	179.15	961.58	5.00	9.18	30.76	1	1	73
Dicrurus leucophaeus	175.15	291.72	3.50	16.58	38.01	2	2	61
Spodiopsar cineraceus	116.00	821.36	6.00	3.51	19.12	8	29	12
Dendrocitta formosae	353.00	137.61	2.00	4.60	30.80	7	10	33
Picus canus	191.50	936.71	9.50	12.95	18.08	4	10	34
Emberiza spodocephala	123.15	676.36	2.50	14.82	15.19	2	2	60
Muscicapa griseisticta	130.00	209.22	2.50	9.35	31.28	3	4	49
Cyanopica cyanus	362.75	571.70	6.50	2.20	35.15	11	35	6
Bambusicola thoracicus	192.75	322.07	8.50	9.35	19.18	3	5	45
Chloris sinica	130.00	671.81	2.50	12.95	19.55	3	8	41
Hemixos castanonotus	106.50	151.83	2.00	8.50	19.21	3	3	52
Micropternus brachyurus	112.00	331.55	5.00	62.39	17.12	1	1	76
Tringa glareola	110.00	961.58	2.00	29.25	31.06	1	1	70
Spizixos semitorques	191.75	333.81	3.50	4.76	15.77	8	12	31
Passer montanus	131.00	961.58	5.50	2.20	12.70	11	34	7
Alcedo atthis	165.50	961.58	6.00	3.51	13.09	2	9	40
Phalacrocorax carbo	798.00	961.58	2.00	514.68	17.36	1	1	69
Horornis fortipes	112.00	263.17	2.00	18.67	12.17	2	4	50
Copsychus saularis	101.50	262.33	5.00	3.54	17.81	9	27	14
Streptopelia orientalis	312.75	961.58	1.00	3.51	31.07	5	33	9
Passer cinnamomeus	117.75	593.90	5.00	29.85	15.15	2	2	59

Table 3. (continued)

Species	Body length (mm)	Geographic range size (km^2)	Clutch size (*n*)	Minimum area requirement (ha)	Dispersal ratio (db)	Habitat specificity (*n*)	Number of parks occupied (*n*)	Nested matrix rank
Anthus hodgsoni	152.00	961.58	5.00	14.82	19.85	2	2	57
Spodiopsar sericeus	115.00	158.15	6.30	3.54	18.26	8	22	16
Cuculus micropterus	319.15	606.69	1.00	4.76	20.21	2	3	55
Turdus mandarinus	158.00	873.91	5.50	2.20	31.28	11	37	2
Muscicapa sibirica	130.75	670.08	2.50	61.38	31.86	1	1	71
Pica pica	211.50	961.58	6.50	2.20	33.39	11	36	5
Tachybaptus ruficollis	158.15	961.58	5.50	3.51	18.92	1	22	17
Dendrocopos canicapillus	155.15	559.19	2.50	3.54	35.03	4	15	27
Nycticorax nycticorax	515.00	821.36	2.00	3.51	31.92	1	16	25
Aegithalos glaucogularis	127.00	738.50	10.50	2.20	30.17	8	32	10
Hierococcyx sparverioides	320.00	110.11	1.00	4.76	29.17	3	15	28
Eudynamys scolopaceus	201.75	162.99	1.00	3.54	32.01	3	13	29
Ardea intermedia	666.50	291.12	2.00	29.25	39.68	1	3	53
Streptopelia chinensis	302.15	595.51	1.00	2.20	17.51	5	37	3
Myophonus caeruleus	305.50	779.68	2.00	160.49	31.76	1	3	54
Lanius schach	128.50	650.92	2.50	4.40	12.59	6	19	21
Sinosuthora webbiana	112.15	261.21	2.50	3.51	11.28	6	30	11

within 1 SD of the predicted curve (Figure 3), rejecting the passive sampling hypothesis.

The nestedness of bird assemblages in Nanjing urban parks also did not result from selective colonization. After controlling for other independent variables, the nestedness of bird assemblages was not correlated with park isolation (Isolation1 and Isolation2) (Table 5) or species dispersal ratio as a proxy for dispersal ability (Table 6).

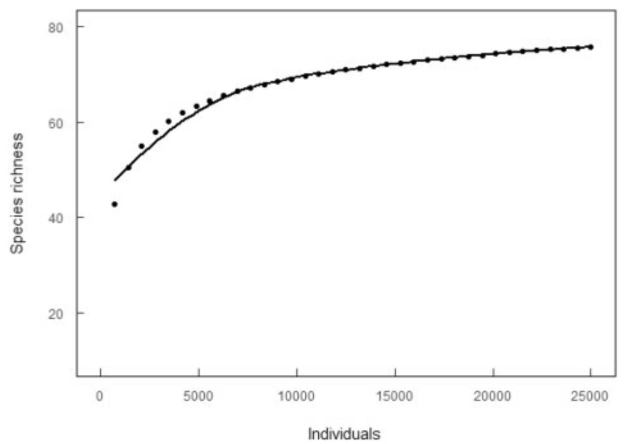

Figure 2. Species accumulation curve for birds in 37 urban parks in Nanjing, China.

Discussion

In this study, we examined the existence of nestedness and underlying causal mechanisms of bird assemblages in a highly urbanized city of Nanjing, China. We found that bird assemblages in Nanjing urban parks were significantly nested. So far, the nestedness pattern was primarily investigated in insular systems, including land-bridge islands and oceanic archipelagoes, or naturally fragmented systems (Cook and Quinn 1995; Wright et al. 1998; Watling and Donnelly 2006). However, to date, only a few nestedness studies have been conducted in urbanized landscapes (Fernández-Juricic 2002; Murgui, 2010; González-Oreja et al. 2012; Lizee et al. 2016). Our study on bird nestedness in urban parks thus contributes to the broad, repeatable ecological generality of nestedness across a wide range of study systems.

We found that the nestedness of bird assemblages in Nanjing urban parks was correlated with park area and species traits associated with extinction risk (minimum area requirement and habitat specificity). The main explanation for the results is that bird species with large area requirement and high habitat specificity have high extinction vulnerability and would disappear first in urban parks, and the selective extinction of bird species will form the nestedness pattern (Schouten et al. 2007; Wang et al. 2010; Xu et al. 2017). Selective extinction was also the main determinant of the nestedness of birds, small mammals, and snakes in the recently inundated Thousand Island Lake (Wang et al. 2010, 2012). Therefore, the nestedness of bird assemblages in Nanjing urban parks conformed to the selective extinction hypothesis.

The habitat-by-site matrix in Nanjing urban parks were found to be highly nested, which was consistent with the habitat nestedness hypothesis. In our study, the nestedness of bird assemblages was also caused by the nested distribution of habitat types in Nanjing urban parks. Several previous studies also found that the habitats for faunal assemblages are nested (Calmé and Desrochers 1999; Wang et al. 2010, 2012, 2013). The habitat nestedness hypothesis is the most obvious process to explain species nestedness because it neglects the dynamic structure of the population and the ecological traits of the species, but directly links the species with their habitats (Calmé and Desrochers 1999; Honnay et al. 1999). Thus, we suggest that future studies should test the habitat nestedness hypothesis when it is possible.

We found that the level of urbanization (building index) also promoted the nestedness of bird assemblages in Nanjing urban parks. This result indicates that bird assemblages in parks with high level of urbanization are proper subsets of parks with low level of urbanization. This is the first time that the nestedness of bird assemblages is linked to the level of urbanization. Therefore, our study revealed a new causal mechanism that influences the nestedness of bird assemblages in urbanized landscapes.

However, the nestedness of bird assemblages in Nanjing urban parks was not correlated with anthropogenic noise. The main reason for this result is probably because most birds recorded in the surveys were common urban birds in our region. In our study, we found that many bird species, such as *Cyanopica cyanus*, *Passer montanus*, *Streptopelias*, *Pycnonotus sinensis*, and *Turdus mandarinus*, inhabited most of the urban parks. Such species living in urban parks may have already adapted to the interference of anthropogenic noise by increasing the frequency or tone of their chirps (Hu and Cardoso 2010). Accordingly, anthropogenic noise had no obvious influences on the nestedness of bird assemblages in our study.

We found that the nestedness of bird assemblages was not correlated with park isolation or species dispersal ability, rejecting the selective colonization hypothesis. At least 2 reasons may explain the weak correlations. First, birds could spread and communicate among different urban parks easily because of their strong dispersal ability, which may greatly reduce the impact of selective colonization on nestedness (McAbendroth et al. 2005; Wang et al. 2013). In addition, the landscape connection provided by wooded streets among different parks allows bird species to communicate more frequently (Fernández-Juricic and Jokimäki 2001). Overall, our results indicate that habitat isolation and dispersal limitation play little role in creating bird nestedness.

The nestedness of bird assemblages in Nanjing urban parks was also not attribute to passive sampling. In fact, the passive sampling hypothesis was rarely supported in previous nestedness studies (Worthen et al. 1998; Wang et al. 2010, 2012; Xu et al. 2017; Li et al. 2019). These studies overall indicate that stochastic process or passive sampling is not a main driver of nestedness. Passive sampling is embedded in some of the null model procedures used to test for nestedness (Andrén 1994; Wright et al. 1998; Higgins et al. 2006). Therefore, the passive sampling effect should be tested first so as to determine whether faunal nestedness results from biological processes.

With the rapid worldwide development of urbanization, the understanding of nestedness and underlying causal mechanisms will provide theoretical basis for the protection of urban biodiversity (Patterson 1987; Ganzhorn and Eisenbeiß 2001; Fleishman et al.

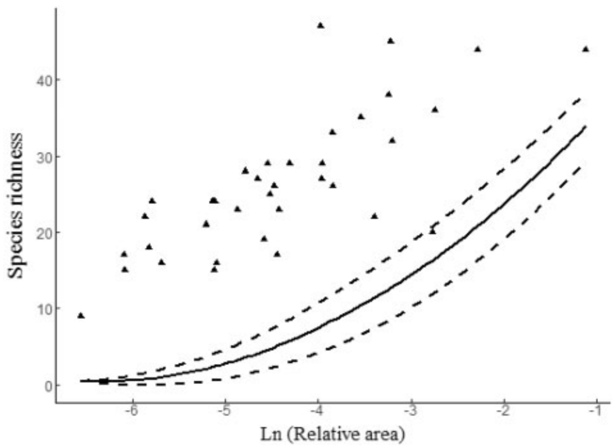

Figure 3. Comparison of observed data to expected values under the random placement model for birds in 37 urban parks in Nanjing, China. Expected values (solid line) and associated standard deviations (±1SD; dashed lines) are shown. Filled triangles represent observed species richness.

Table 4. Results of nestedness analyses using the program NODF conducted on the species-by-site matrix for bird assemblages and their habitats in 37 urban parks in Nanjing, China

Species nestedness				Habitat nestedness		
	Observed	Expected	*P*-value	Observed	Expected	*P*-value
NODF	64.03	75.11	<0.001	77.71	46.85	<0.001
NODFc	75.86	84.25	<0.001	76.60	46.69	<0.001
NODFr	61.26	72.97	<0.001	88.87	48.39	<0.001
WNODF	43.70	58.03	<0.001			
WNODFc	47.66	58.22	<0.001			
WNODFr	42.78	58.01	<0.001			

Table 5. Partial Spearman rank correlations between rank orders of sites using the program NODF and orders of sites after rearranging the matrix according to each habitat variable

Park area (ha)	Noise (dBA)	Isolation1 (m)	Isolation2 (m)	Number of habitat types (n)	Building index
−0.469**	0.337	−0.168	0.177	−0.626***	0.402*

Referred to Table 1 for the interpretation of variables., **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

Table 6. Partial Spearman rank correlations between rank orders of species using the program NODF and orders of species after rearranging the matrix according to each ecological trait

Body length (mm)	Geographic range size (km^2)	Clutch size (*n*)	Minimum area requirement (ha)	Dispersal ratio (dp)	Habitat specificity (*n*)
−0.223	−0.078	0.021	0.817***	−0.020	−0.529***

****P* < 0.001 .

2007). Our results have several general and specific implications for the park planning and bird diversity conservation in the Nanjing region. First, parks with large area should be conserved because park area is the main driver of bird nestedness in our system. Second, we should pay more attention to parks with diverse habitats because habitats for birds are highly nested and habitat diversity has impacts on species nestedness (Wang et al. 2013). In addition, reducing the level of urbanization is crucial for the protection of bird diversity as building index promotes nestedness in our system. Overall, we suggest that conservation priority should be given to parks with large area, rich habitat diversity, and less building index. Finally, we found that bird species with large area requirement and high habitat specificity, such as *Phalacrocorax carbo*, *Myophonus caeruleus*, *Micropternus brachyurus*, had high extinction risk. Therefore, such extinction vulnerable species should be conserved priorly to prevent future local extinctions.

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Authors' contributions

Y.W. conceived and designed the study. X.T. and X.Y. collected the data. X.T. analyzed the data with assistance from C.C. and wrote the first draft of the article. Y.W. contributed substantially to the writing of the article. All authors read and approved the final article.

Supplementary material

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

Conflict of interest

The authors declare that they have no competing interests. The funders have no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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