# Nest site selection for five common birds and their coexistence in an urban habitat

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## HIGHLIGHTS

- The trees of artificial green belts seem to be the best breeding habitat for urban birds.
- Birds' breeding success relies on the trade-off of bird reproduction between the benefit and the expense from urban habitats.
- The successful coexistence of bird species in urban habitats is on account of differences in resources utilization.

## GRAPHICAL ABSTRACT
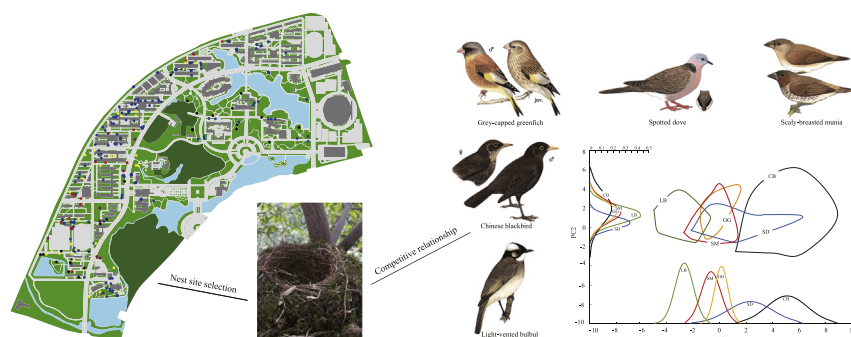
## ABSTRACT

Many species of birds gradually adapt to urbanization and colonize cities successfully. However, their nest site selection and competitive relationship in an urban community remain little known. Understanding the impact of urbanization on birds and the competitive relationship has important implications for the conservation and management of wildlife in urban ecosystems. Here, we undertook a systematic study to quantify nests in all species of birds in an urbanizing area of Nanchang, China. A total of 363 nests were detected in surveys including 340 nests of 16 bird species and 23 unidentified species nests. We mainly analyzed 5 dominant breeding birds with a sample size of >10 during the two breeding seasons (From April to July in 2016 and 2017), which included the light-vented bulbul, Chinese blackbird, scaly-breasted munia, spotted dove and grey-capped greenfinch. Most birds (93.66%) nested in the tree of artificial green belts, which seems to be the best breeding habitat for urban birds. Our results suggested that birds' breeding success relies on the trade-off between the benefit and the expense of specific stresses from habitats. The nest site selection of birds is also affected by the life habit of urban predators. Furthermore, competition among species can influence their distributions and utilization of environmental resources when birds nest in cities. We confirmed that the niche differentiation of five bird species in an urban environment makes them coexist successfully by utilizing various resources.

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# 1. Introduction

The expansion of urban areas is considered to have one of the most important anthropogenic impacts on the Earth's ecosystem (Aronson et al., 2014; Foley et al., 2005; Groom et al., 2006), by dramatically changing the natural habitat structure, ecosystem functioning and biodiversity (Forman, 2014; Gaston et al., 2010; Gil and Brumm, 2014; Grimm et al., 2008). Many animal species live in urban areas, where they encounter human-altered environmental conditions (Arroyo-Solís et al., 2013; Kivelä et al., 2014). Urbanization poses many challenges to organisms because it integrates a wide array of drastic environmental alterations, including the replacement and fragmentation of natural vegetation, the alteration of the community of predators and food sources, and an increase in human disturbances and pollution with regarding to nighttime lights, chemicals, and noise (Lowry et al., 2012; Sol et al., 2013). Although urbanization often adversely affects and even causes extinction of some native species and makes homogenization of avian communities (Husté and Boulinier, 2007; McKinney, 2006; Sol et al., 2014; Soulé et al., 1988), increasingly more worldwide birds are colonizing and adapting to new urban environments (Francis and Chadwick, 2012; Luniak, 2004; Møller, 2009). There is rapidly increasing interest in studying how species colonize urban habitats (Gaston et al., 2010; Gil and Brumm, 2014; Lepczyk and Warren, 2012). However, the way that most bird species from rural areas and forests adapt and respond to urbanization remains poorly understood. Urbanization changes some of the resources that birds (in especial similar, ecologically and taxonomically species) depend on (Gaston et al., 2010; Ibáñez-Álamo and Soler, 2010), such as the type and availability of the nest site (Beissinger and Osborne, 1982; Wang et al., 2009). When birds live in cities, they have to adjust their behavior and life histories to novel environments (Morelli et al., 2018). Noise and artificial light pollution have some negative effects on birds, and they must change their behavior to adapt to urban environments (Nemeth et al., 2013; Sun et al., 2017). Meanwhile, some animals are likely to have advantageous traits that allow them to profit from human-derived food sources in the city (Sol et al., 2011). The populations of some species in urban habitats and forests differ from one another in terms of genetics, breeding, behavioral syndrome and ecological features (Martin and Bonier, 2018; Kontsiotis et al., 2019; Callaghan et al., 2019; Sepp et al., 2018) Therefore, to colonize and breed successfully in urban environments, individuals must have trade-offs between these urban specific stresses and benefits from these new habitats (Grinnell, 1924; Wang et al., 2015).

However, birds not only have to adapt to the human environment, they also face competitions with different species in urban area in many conditions, including food, space, etc. The niche theory states that two species settle in the same area cannot have identical niches (Gause, 1934). Two species competing for the same niche cannot coexist stably at the same time, and the differentiation of niche is the premise of species coexistence in the community (Tokeshi, 2009; Zheng, 1995). If species had no influence on each other's resource utilization their niches would still differ, competition should result in an overdispersion of niches in niche-space (Schoener, 1974; Tokeshi, 2009).

Recently, some studies have focused on the nest site selection of one bird species in urban areas, including Passeriformes (Jokimäki et al., 2017; Wang et al., 2015), Pelecaniformes (Gantz and Yañez, 2016; Singh and Downs, 2016) and Accipitriformes (Kumar et al., 2017; Mcpherson et al., 2016). However, these studies have only investigated the impact of urbanization on nesting at the individual level. The habitat type of studies covered almost all of city, such as urban parks (Dodaro and Battisti, 2014; Romero et al., 2015; Wysocki, 2014), urban mosaic (Mcpherson et al., 2016) and multiscale of urban environment (Teglhøj, 2017; White et al., 2017). There are also some studies that focused on the nest site selection of various bird species, but concentrating upon some guilds (e.g. heronry species reported by Roshnath and Sinu, 2017 and raptors reported by Mcpherson et al., 2016). Although some studies have reported the nest site selection of all birds in an urban community, they have only compared the similarities and differences among various guilds (Rao and Koli, 2017). Competition among urban birds often involves direct aggression, coexistence and community structure (Peiman and Robinson, 2010; Tokeshi, 2009). Plenty of researches have studied on the bird species competition of urban resource utilization, including invasive and native species (González-Oreja et al., 2018; Lill and Muscat, 2015; Thibault et al., 2018), dominant and subordinate species (Martin and Bonier, 2018), and two or three related species (Ballejo et al., 2018; Galbraith et al., 2017). However, the competitive relationship of species in a developing urban community remains little known.

Accompanied with the rapid urbanization in China, many common bird species gradually adapt to breed successfully in the urban environments. The adjustment in nesting behaviors such as nest site shifts may reflect the ability of birds to adapt to urban ecosystems (Luniak, 2004; Wang et al., 2009). Plenty of environmental features can act as a selection pressure or factor affecting the nest site, thereby nest site selection affecting the survival, reproduction and fitness of birds (Kivelä et al., 2014; Sepp et al., 2018). Given the challenges of urbanization, competitive interactions may be important for determining which species persist or thrive in cities (Gil and Brumm, 2014; Lepczyk and Warren, 2012; Martin and Bonier, 2018; Marzluff et al., 2001). Here, we undertook a systematic study to quantify nests in all species of birds in an urban habitat and our objectives were to test the hypotheses that (1) most of birds nested in the tree of artificial green belts due to abundant foods and few predators, and (2) the different avian species could coexist successfully by utilizing various resources in an urban environment.

# 2. Methods

## 2.1. Study area

The survey was carried out in a 300-ha study area (841.1 m a.s.l., 115° 47′ 12″ – 115° 38′ 34″ E, 28° 39′ 4″ – 28° 40′ 16″ N) with a population of 55,000, Nanchang City, Jiangxi Province, China (Fig. 1). The climate is subtropical humid monsoon, and the annual precipitation is 1600–1700 mm. The survey area that is located on edge of Nanchang City, and its main types of land are artificial habitats. The habitat in the study region, based on their differences in building indexes and vegetation categories, can be classified into five main types, i.e. road pavements, manmade lakes, artificial green belts, secondary forests and buildings (Fig. 1).

## 2.2. Nest monitoring and habitat measurements

Nest site surveys were performed during the two bird breeding seasons (from March to July in 2016 and 2017), which begin according to local information on the phenology of breeding birds and are repeated once a week to find new nests and to measure nests that end or fail in breeding. Each time, we investigated the entire study area to check whether there was a new nest. All nests found were marked with membered plastic tags and recorded longitude and latitude to avoid duplicating records in the second breeding season of the survey. A total of 14 parameters related to bird reproduction were collected, including 10 environmental factors and 4 nest factors (Table 1). When a new nest was found at the first time, we recorded the bird species, the location of nest sites and the tree species if the bird nested in a tree. The remaining parameters were measured after breeding without disturbing the nesting bird.

According to the methods as described in Lahaye and Gutiérrez (1999), and Yeldell et al. (2017), we measured all parameters during the breeding season. The tree height (TH, m) and the nest site height (NSH, m) were measured using an infrared rangefinder (DISTO X310, Leica, Hungary). The nest inside diameter (NID, cm); the nest outside
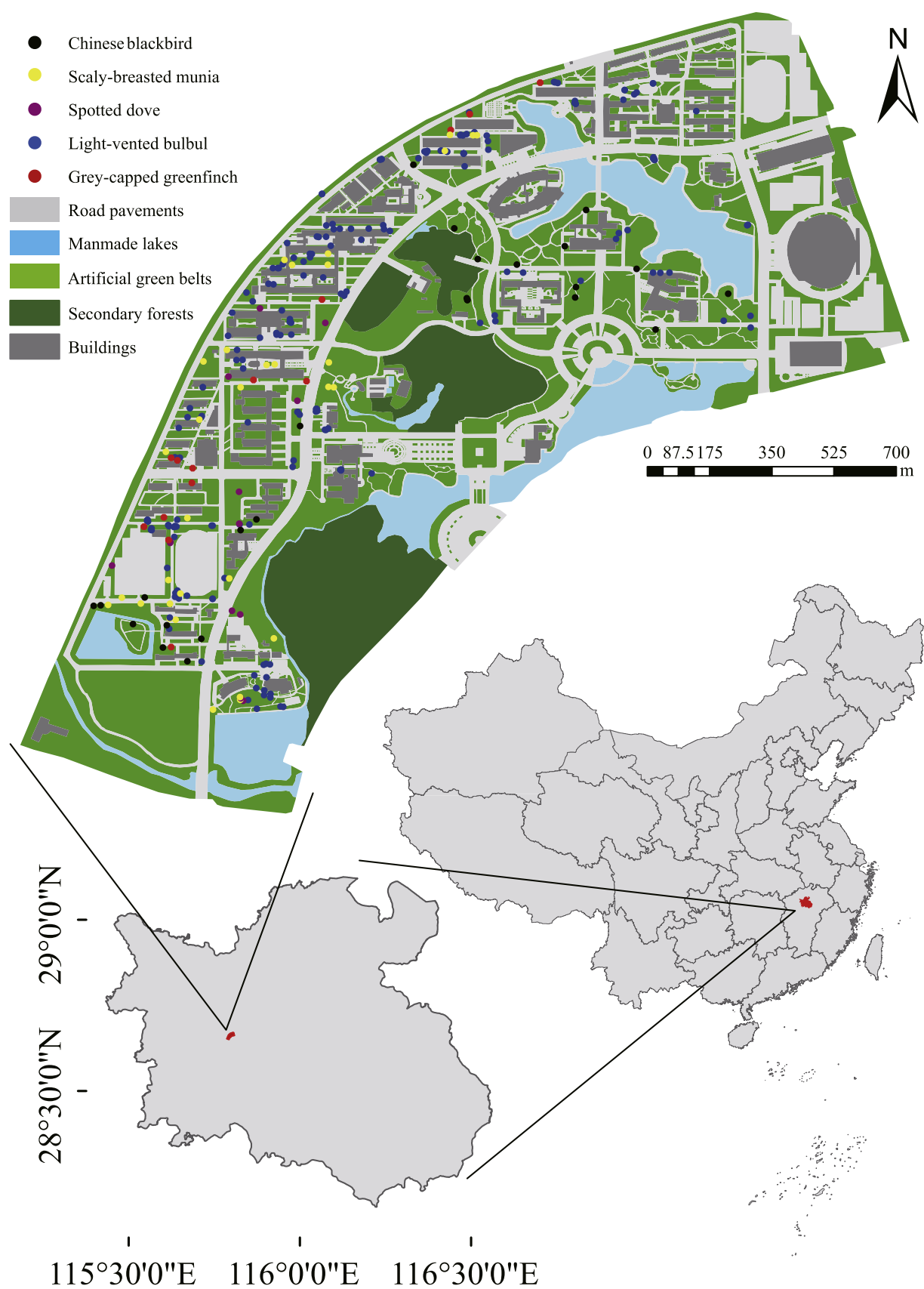
**Fig. 1.** Location and land use of the study area including five species nest sites in Nanchang in China.

**Table 1**
Values (mean ± SD number) of different nest site characteristics of five bird species and the ANOVA and Duncan's new multiple range test.

| Variable Name | Mean (± SD) | | | | |
|---|---|---|---|---|---|
| | LB | CB | SM | SD | GG |
| TH (m) | 3.03 ± 0.84[a], n = 206 | 8.40 ± 2.35[d], *n* = 33 | 3.91 ± 0.99[b], n = 32 | 5.13 ± 2.21[c], n = 17 | 3.99 ± 1.01[b], *n* = 14 |
| GD (cm) | 12.10 ± 3.76[a], n = 206 | 24.26 ± 14.17[c], n = 33 | 13.04 ± 4.09[a], *n* = 30 | 18.04 ± 8.68[bc], n = 17 | 14.38 ± 5.04[ab], n = 14 |
| DTC (m) | 2.16 ± 0.62[a], n = 206 | 6.24 ± 1.95[d], n = 33 | 3.11 ± 1.00[b], n = 32 | 4.03 ± 1.45[c], n = 17 | 3.19 ± 0.86[b], n = 14 |
| DR (m) | 5.05 ± 4.10[a], n = 206 | 65.48 ± 65.19[b], n = 33 | 6.64 ± 4.61[a], n = 32 | 7.69 ± 6.46[a], n = 17 | 5.13 ± 4.03[a], n = 14 |
| DW (m) | 142.37 ± 66.13[b], n = 206 | 38.03 ± 50.58[a], n = 33 | 141.32 ± 64.39[b], n = 32 | 141.45 ± 98.77[b], n = 17 | 157.18 ± 62.05[b], n = 14 |
| MSI (m) | 20.81 ± 33.97[a], n = 206 | 93.12 ± 77.22[b], n = 33 | 74.90 ± 125.37[b], n = 32 | 91.86 ± 131.22[b], n = 17 | 172.45 ± 248.87[c], n = 14 |
| MSII (m) | 87.67 ± 80.29[bc], n = 206 | 113.41 ± 124.08[c], n = 33 | 28.72 ± 22.52[a], n = 32 | 27.96 ± 36.31[a], n = 17 | 47.52 ± 61.56[ab], n = 14 |
| PCC (%) | 89.96 ± 12.06[b], n = 205 | 82.82 ± 14.98[ab], n = 33 | 87.03 ± 20.95[b], n = 31 | 87.24 ± 8.93[b], n = 17 | 78.7 ± 12.86[a], n = 14 |
| CC (%) | 89.99 ± 11.84[b], n = 205 | 57.33 ± 17.19[a], n = 33 | 79.53 ± 23.52[b], n = 31 | 86.30 ± 11.12[b], n = 17 | 86.25 ± 16.33[b], n = 14 |
| IBPP (%) | 79.72 ± 20.98[a], n = 206 | 38.98 ± 34.31[a], n = 33 | 42.95 ± 26.08[a], n = 32 | 32.39 ± 24.39[a], n = 17 | 43.48 ± 25.14[a], n = 14 |
| NSH (m) | 2.01 ± 0.75[a], n = 206 | 5.89 ± 2.49[d], n = 33 | 2.86 ± 0.89[b], n = 32 | 3.79 ± 1.89[c], n = 17 | 2.82 ± 0.98[b], n = 14 |
| NID (cm) | 7.27 ± 2.02[b], n = 206 | 13.00 ± 1.90[e], n = 33 | 5.08 ± 3.51[a], n = 32 | 11.62 ± 5.12[c], n = 17 | 5.94 ± 1.86[ab], n = 14 |
| NOD (cm) | 10.15 ± 1.80[a], n = 206 | 15.77 ± 1.58[b], n = 33 | 17.27 ± 8.22[b], n = 32 | 15.54 ± 3.72[b], n = 17 | 8.92 ± 2.15[a], n = 14 |
| ND (cm) | 5.46 ± 2.49[b], n = 206 | 7.29 ± 1.28[c], n = 33 | 12.25 ± 3.26[d], n = 32 | 3.8 ± 3.63[a], n = 17 | 4.12 ± 1.73[ab], n = 14 |

Significant difference at the 0.05 level. a, b, c and d represent different groups respectively, and there is significant difference between a, b, c and d groups. LB = Light-vented Bulbul, CB = Chinese Blackbird, SM = Scaly-breasted Munia, SD = Spotted Dove, and GG = Grey-capped Greenfinch. TH = Tree height, GD = Ground diameter, DTC = Diameter of tree canopy, DR = Distance to road, DW = Distance to water sources, MSI = Minimum spacing of intraspecific nest, MSII = Minimum spacing of interspecific nest, PCC = Percent canopy cover, CC = Concealment, IBPP = Index of building and pavement proportion, NSH = Nest site height, NID = Nest inside diameter, NOD = Nest outside diameter, ND = Nest depth.

diameter (NOD cm) and the nest depth (ND, cm) were measured using a straightedge. The ground diameter (the diameter around the base of the tree trunk; GD, cm); the diameter of the tree canopy (DTC, m, the mean of long and short diameters); the distance to road (DR, m); the distance to water sources (DW, m) which are perennially watery, including artificial lakes, ponds, rivers and ditches; the minimum spacing of the intraspecific nest (MSI, m); and the minimum spacing of the interspecific nest (MSII, m) were obtained by using a tape-measure, and the GPS measurements on Google Earth were carried out when the distance was too far to obtain. A measurement of the percent of canopy cover (PCC, %) was estimated only on a sunny day by using a tape-measure to measure the length of two diagonal shades of canopy. The concealment (CC, %) was estimated by using photos which include four directions of the nest within 1 m range (the percentage of whole the nest unexposed area in the photos was estimated, then, the mean values were calculated). We also used program ArcGIS (version 10.1) to calculate the building and pavement proportion (Index of the Building and Pavement Proportion, IBPP, %) of each nest at increasing spatial scales (0-5 m, 0-10 m, 0-20 m, 0-30 m, and 0-40 m, 0-50 m), as follows: IBPP = 1 building and pavement proportion 5 m + 0.5 building and pavement proportion 10 m + 0.25 building and pavement proportion 20 m + 0.125 building and pavement proportion 30 m + 0.0625 building and pavement proportion 40 m + 0.3125 building and pavement proportion 50 m (Lan et al., 2013; Melles et al., 2003).

### 2.3. Statistical analysis

The dataset of 11 species were removed from further analyses for the small sample size (<10 nests). Then the five species of birds, light-vented bulbul (*Pycnonotus sinensis*), Chinese blackbird (*Turdus mandarinus*), scaly-breasted munia (*Lonchura punctulate*), spotted dove (*Spilopelia chinensis*), and grey-capped greenfinch (*Chloris sinica*) were retained for the next analysis. In total, data of 312 nests (143 nests in 2016 including 88 nests of light-vented bulbul, 21 nests of Chinese blackbird, 21 nests of scaly-breasted munia, 9 nests of spotted dove and 4 nests of grey-capped greenfinch; 169 nests in 2017 including 128 nests of light-vented bulbul, 12 nests of Chinese blackbird, 11nests of scaly-breasted munia, 8 nests spotted dove and 10 nests of grey-capped greenfinch) were merged in a single data pool. Nest site characteristics of five bird species included 14 variables (Table 1). Normality of the distributions was assessed using the Kolmogorov-Smirnov test with the significance level set at 0.05 (Lilliefors, 1967). When the data were not normally distributed (Appendix Table A), Spearman's rank correlation test was performed to assess the correlation among the nesting parameters (Appendix Table B) (Maritz, 1995). The one-way analysis of variance (ANOVA) test and Duncan's new multiple range test (Hsu, 1996) were used to evaluate the difference between the nest site characteristics of five species.

A principal component analysis (PCA, Conner and Adkisson, 1977) was used to analyze the variation within and among these variables with response to different species of birds. Because the value of the principal component score was nonnormal distribution, we used the method described by Sheppard (2003) to convert data to a normal distribution in Program Excel 2016 by using the 'norm.dist' function. Then, we plotted the ecological amplitudes of the first principal component and the second principal component, respectively (Fig. 4).

After non-significant difference test between 2016 and 2017 (Appendix Table C), the data from two years were merged in a single data pool. We used a logistic regression (Hastie, 2017) to predict nest site selection and to evaluate the influence of variables on nest site selection, with used or nonused (used by other bird species) trees as the dependent variable criterion. To reduce over-fitting caused by redundant variables, we selected the most explanatory and uncorrelated variables, then eliminated the others based on the highest correlation coefficients (Spearman's rank correlation, |*r*| > 0.70; Inselman et al., 2015; Soh et al., 2002). Then, the variables that provided the most meaningful biological interpretation were retained and the others were removed from further analyses, which resulted in a set of 9 variables (including GD, PCC, NSH, CC, MSI, MSII, DR, DW and BIPP). We used Akaike Information Criterion corrected for a small sample size ($AIC_c$) model selection and calculated the $AIC_c$ difference ($\Delta AIC_c$) between the model with the lowest $AIC_c$ value and all models for each model (Melles et al., 2003). Models with $\Delta AIC_c < 2$ have support for being the best model in a set. We also used Akaike weights ($w_i$) as an indication of the support for each model. $AIC_c$ values only indicate the relative strength of models in a set (Burnham and Anderson, 2004), so we also considered the area under the receiver operating characteristic (ROC) curve as metrics of the model fit. ROC curve (known as the AUC) is widely used to estimate the predictive accuracy of distributional models derived from presence–absence species data (Fawcett, 2006; Lobo, 2007; Krzanowski and Hand, 2009). The ROC plot can constitute a very informative and powerful tool for assessing and comparing predictive models (see Fawcett, 2006; Krzanowski and Hand, 2009). Hosmer and Lemeshow (Hosmer et al., 1989) considered models with an area under ROC curve values (AUC) between 0.7 and 0.8 to have 'acceptable discrimination' and those with values between 0.8 and 0.9 to have 'excellent discrimination'. We used Program R 3.5.1 (R Core Team, 2016) for all statistical analyses.

# 3. Results

## 3.1. Bird species and nesting tree species

A total of 363 nests (164 in 2016 and 199 in 2017, Appendix Table D), including 340 nests of 16 bird species (13 Passeriformes and 3 Pelecaniformes) and 23 unidentified species nests (Fig. 2), were detected in the surveys. The largest number of nests belonged to light-vented bulbul's ($n = 206$), which accounted for 56.75% of the total. The most nests were found in the tree of artificial green belts ($n = 340$), 93.66% of the total, while 3.86% nests were found in buildings ($n = 14$) and 2.48% nests were found in the tree of secondary forests ($n = 9$). Almost five species of birds nested in 12 species of trees ($n = 301$) (Fig. 1), whereas only one nest of the Chinese blackbird was found in the building. The most light-vented bulbul nested in the trees of *Camellia japonica* (92.23%, $n = 190$). The majority of Chinese blackbird nested in trees of *Cinnamomum camphora* (63.64%, $n = 21$) and *Elaeocarpus decipiens* (18.18%, $n = 6$). Differently, three species, including scaly-breasted munia, spotted dove and grey-capped greenfinch showed no apparently preference to any special tree species.

## 3.2. Environmental factors and predators

In a comparison of different characteristics among five species of birds, the ANOVA and Duncan's new multiple range test showed significant difference among most nest site characteristics of five species (Table 1). Studies on the factors of the nesting tree, including the highest values of TH ($8.40 \pm 2.35$ m); GD ($24.26 \pm 14.17$ cm); DTC ($6.24 \pm 1.95$ m); and NSH ($5.89 \pm 2.49$ m) belonged to the Chinese blackbird, whereas the lowest values of these factors were all found in the light-vented bulbul (TH = $3.03 \pm 0.84$ m, GD = $12.10 \pm 3.76$ cm, DTC = $2.16 \pm 0.62$ m, NSH = $2.01 + 0.75$ m). The Chinese blackbird usually nested far away from the road (DR = $65.48 \pm 65.19$ m) and close to water sources (DW = $38.03 \pm 50.58$). Conversely, the other four species nested close to the road (light-vented bulbul = $5.05 \pm 4.10$ m, scaly-breasted munia = $6.64 \pm 4.61$ m, spotted dove = $7.69 \pm 6.46$ m, grey-capped greenfinch = $5.13 \pm 4.03$ m) and far away from water sources (light-vented bulbul = $142.37 \pm 66.13$ m, scaly-breasted munia = $141.32 \pm 64.39$ m, spotted dove = $141.45 \pm 98.77$ m, grey-capped greenfinch = $157.18 \pm 62.05$ m). The results of the minimum spacing of nest showed that grey-capped greenfinch prefer to breed dispersedly (MSI = $172.45 \pm 248.87$ m), while light-vented bulbul breed centrally (MSI = $20.81 \pm 33.97$ m). For spacing of the interspecific nests, Chinese blackbirds nested farthest from other species (MSII = $113.41 \pm 124.08$ m), whereas scaly-breasted munia (MSII = $28.72 \pm 22.52$ m) and spotted dove (MSII = $27.96 \pm 36.31$ m) had the nearest MSII. For nest concealment, light-vented bulbul owned the highest values of PCC ($89.959 \pm 12.06\%$) and CC ($89.99 \pm 11.84\%$), while Chinese blackbird had the lowest values of CC ($57.33 \pm 17.19\%$) and grey-capped greenfinch had the lowest values of PCC ($78.7 \pm 12.86\%$). Scaly-breasted munia (NOD = $17.27 \pm 8.22$ cm), Chinese blackbird (NOD = $15.77 \pm 1.58$ cm) and spotted dove (NOD = $15.54 \pm 3.72$ cm) bred with the biggest nests, whereas light-vented bulbul (NOD = $10.15 \pm 1.80$ cm) and grey-capped greenfinch (NOD = $8.92 \pm 2.15$ cm) bred with the smallest nests. Scaly-breasted munia bred with the deepest nest (ND = $12.25 \pm 3.26$ cm), while spotted dove bred with the shallowest nest (ND = $3.8 \pm 3.63$). In addition, spotted dove and scaly-breasted munia used only one main material for nesting, but the other three species used many materials for nesting, including artificial materials.

In addition, we recorded a total of five species predators from the ground in surveys, including one king ratsnake (*Elaphe carinata*), one red-banded snake (*Dinodon rufozonatum*) and three buff-breasted rats (*Rattus flavipectus*).

## 3.3. Species niches

The PCA performed on the nest site characteristics variables yielded three principal components, together explaining 60.348% of the total variation in the analyzed sample (Table 2). The first component PC1 accounted for 35.509% of the total variance. The highest correlations with characteristics correspond to TH (0.927), GD (0.642), DTC (0.919), CC (0.642) and NSH (0.770), which were all positively correlated to the nest site selection. The second component PC2 accounted for an additional 13.468% of the total variance. This component was negatively correlated with PCC (−0.718), and the highest correlations with characteristics correspond to DW (0.666). The third component PC3 accounted for 11.370% of the total variance. The MSII (0.709) was highly positively correlated with the third component.

The nest site relationships among the five species can be observed when the mean values for each species are plotted on the 3 components (Fig. 3). Obviously, light-vented bulbul and Chinese blackbird were more dispersed, while the other three species, scaly-breasted munia, spotted dove and grey-capped greenfinch were more concentrated. In the first component, Chinese blackbird had the highest value (mean = 7.116), while light-vented bulbul had the lowest value (mean = −2.086). The values of the other three species were closer in this component. In the second component, grey-capped greenfinch had the highest values (mean = 1.145), whereas Chinese blackbird had the lowest (mean = −0.821). The other three species were in the central position between them. In the third component, scaly-breasted munia (mean = −1.152), spotted dove (mean = −1.102) and grey-capped greenfinch (mean = −1.369) had the lower values, while light-vented bulbul (mean = 0.484) and Chinese blackbird (mean = 0.104) had the higher values.

For nest niche distribution analyses, the nest site of each species was plotted on the first and second principal components and each was circled to obtain a visual estimation of overlap (Fig. 4). In the first component, an extensive overlap among spotted dove and the other four species was obvious. Conversely, there was no overlap between light-vented bulbul and Chinese blackbird. The niches used by the spotted dove and Chinese blackbird were much wider than those used by the other species. The overlap area was the largest between scaly-breasted munia and grey-capped greenfinch, which indicated the similar nest niches between these two species. However, in the second component, all five species were overlapped. When we circled the nest sites to obtain a visual estimation overlap with the first and the second principal components, there was no overlap between the Chinese blackbird and light-vented bulbul. However, some moderate overlaps were found among light-vented bulbul, scaly-breasted munia, grey-capped greenfinch and spotted dove. Species of the spotted dove overlapped with the other four species, and the Chinese blackbird merely overlapped a little with the spotted dove.

## 3.4. Nest site selection models

We identified one of the best nest site selection models (top-rank model, $\Delta AIC_C = 0$) among the five species, respectively (Table 3). There were eight variables in all top-rank models of five species (Fig. 5). The factors, including GD, MSI and MSII, appeared in four models; whereas NSH and DR appeared in three models; and DW, PCC and CC appeared in only two models.

The results of logistic regression indicated that the model ($w_i = 0.708$) [NSH + MSI + MSII + DR + DW] was the top-ranked model for predicting the nest site selection of the light-vented bulbul, and the predictive capability of the model was excellent (AUC = 0.959, Appendix Fig. A1). All parameters in this model had significant effects (Appendix Table E). The model ($w_i = 0.331$) [NSH + GD + CC + MSI + MSII+ DW] was the best model for predicting the nest site selection of the Chinese blackbird, and the predictive capability of the model was excellent (AUC = 0.973, Appendix Fig. A2), where all factors except MSI ($z =$
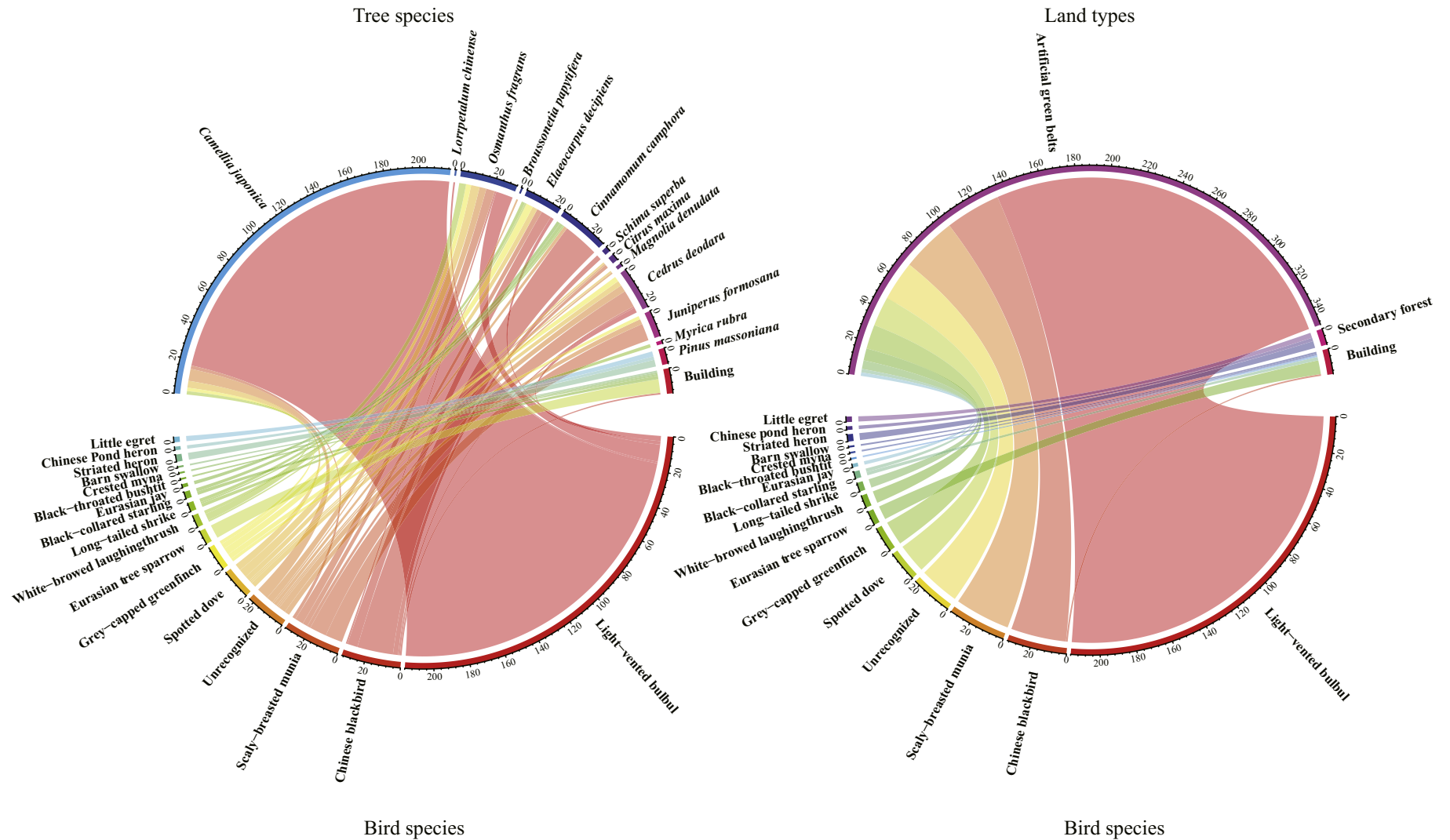
**Fig. 2.** Total number of all bird species' nests recorded during the study period with different nesting sites (16 species of birds; light-vented bulbul *Pycnonotus sinensis*, Chinese blackbird *Turdus Mandarinus*, scaly-breasted munia *Lonchura punctulata*, spotted dove *Spilopelia chinensis*, grey-capped greenfinch *Chloris sinica*, white-browed laughingthrush *Garrulax sannio*, Eurasian tree sparrow *Passer montanus*, long-tailed shrike *Lanius schach*, black-collared starling *Gracupica nigricollis*, Eurasian jay *Garrulus glandarius*, black-throated bushtit *Aegithalos concinnus*, crested myna *Acridotheres cristatellus*, barn swallow *Hirundo rustica*, striated heron *Butorides striata*, Chinese pond heron *Ardeola bacchus* and little egret *Egretta garzetta*).

**Table 2**
Principal component loading for nest site variables.

| | Component | | |
|---|---|---|---|
| | PC1 | PC2 | PC3 |
| Total variance | 3.766 | 1.482 | 1.251 |
| Percentage total variance (%) | 35.509 | 13.468 | 11.370 |
| Cumulative percentage total (%) | 35.509 | 48.978 | 60.348 |
| Correlation of components to nest site variables | | | |
| TH | **0.927** | 0.054 | 0.480 |
| GD | **0.642** | 0.339 | 0.308 |
| PCC | −0.147 | **−0.718** | 0.080 |
| DTC | **0.919** | 0.018 | 0.058 |
| CC | **0.642** | −0.127 | −0.512 |
| MSI | 0.387 | 0.332 | −4.68 |
| MSII | 0.023 | 0.028 | **0.709** |
| DR | 0.589 | −0.442 | −0.510 |
| DW | −0.504 | **0.666** | −0.158 |
| NSH | **0.770** | 0.230 | 0.245 |
| IBPP | −0.105 | 0.170 | 0.269 |

Loading of variable with absolute value > 0.6 are marked in bold. Variable descriptions are found in Table 1.

−0.872, $p = 0.383$) had significant effects in this model (Appendix Table E). The best model ($w_i = 0.665$) of the scaly-breasted munia was [GD + MSII + DR], and the predictive capability of the model was acceptable (AUC = 0.737, Appendix Fig. A3). All parameters had significant effects in this model (Appendix Table E). The top-ranked model ($w_i = 0.542$) of the spotted dove was [GD + PCC + MSI + MSII + DR], and the predictive capability of the model was acceptable (AUC = 0.779, Appendix Fig. A4), where all factors except PCC ($z = 1.294$, $p = 0.196$) had

significant effects (Appendix Table E). The best model ($w_i = 0.265$) of the grey-capped greenfinch contained five variables [NSH + GD + PCC + CC + MSI], and the predictive capability of the model was acceptable (AUC = 0.765, Appendix Fig. A5). All parameters in this model had significant effects (Appendix Table E).

## 4. Discussion

Using pseudo-absences may lead to biased AUC values, because this index gives equal weights to omission and commission errors and pseudo-absences tend to inflate the number of false absences ignoring its properties and flaws can distort and bias our perception of model performances (Lobo, n.d.; Alberto, 2012). The values of AUC could be dependent on the N of the observations, which is very heterogeneous among bird species in this study. But we still used the AUC values in the study, because using independent validation data to assess model predictions favored nest site selection and it was indicating important information about the model's performance.

### 4.1. The trade-offs of nest site selection for birds in an urban habitat

Where and how birds breed successfully relies on the trade-off between the benefit and the expense of specific stresses from urban habitats. Urban areas as a source of novel conditions, offer possibilities for species that approve coping with the challenges of changing environments (Carbó-Ramírez et al., 2015; Luniak, 2004; Partecke et al., 2006). Urbanization dramatic alters historical habitats within which species have evolved (Alberti et al., 2017; Johnson and Munshi-South,
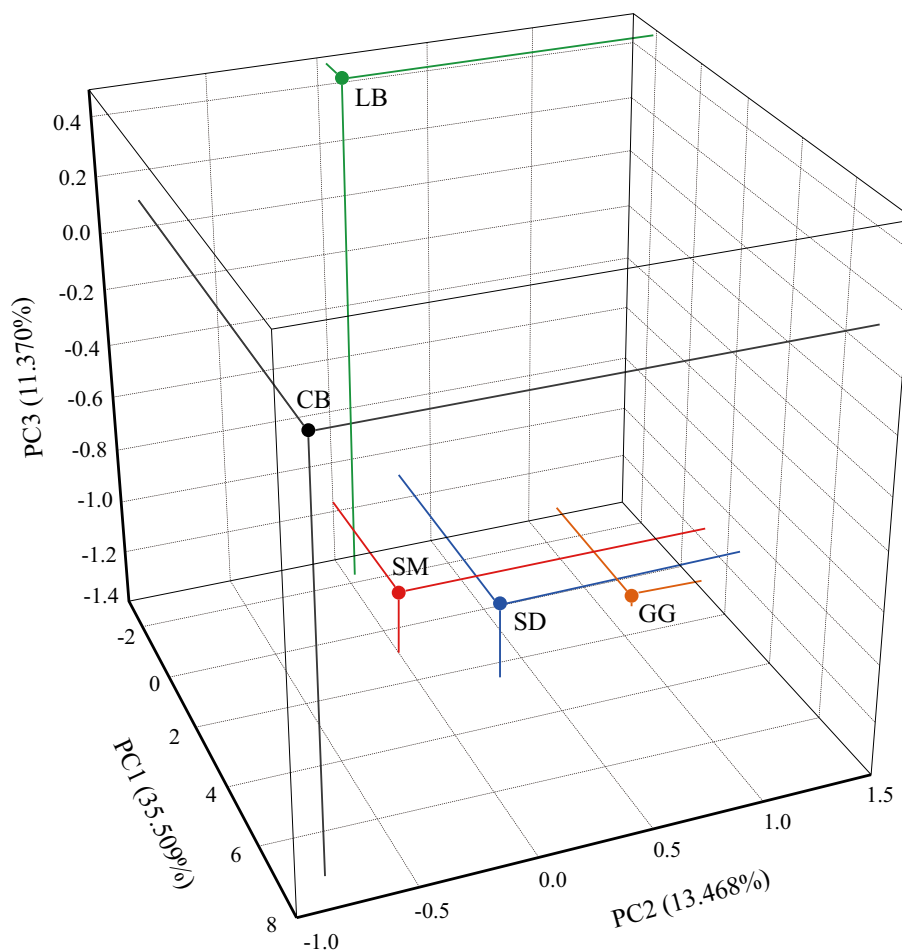


**Fig. 3.** Three dimensional ordinations of nest site selection among five bird species on the first three principal components. Contribution of variables to each component is summarized in the text (Dots indicate mean, LB = light-vented bulbul, CB = Chinese blackbird, SM = scaly-breasted munia, SD = spotted dove, and GG = grey-capped greenfinch).
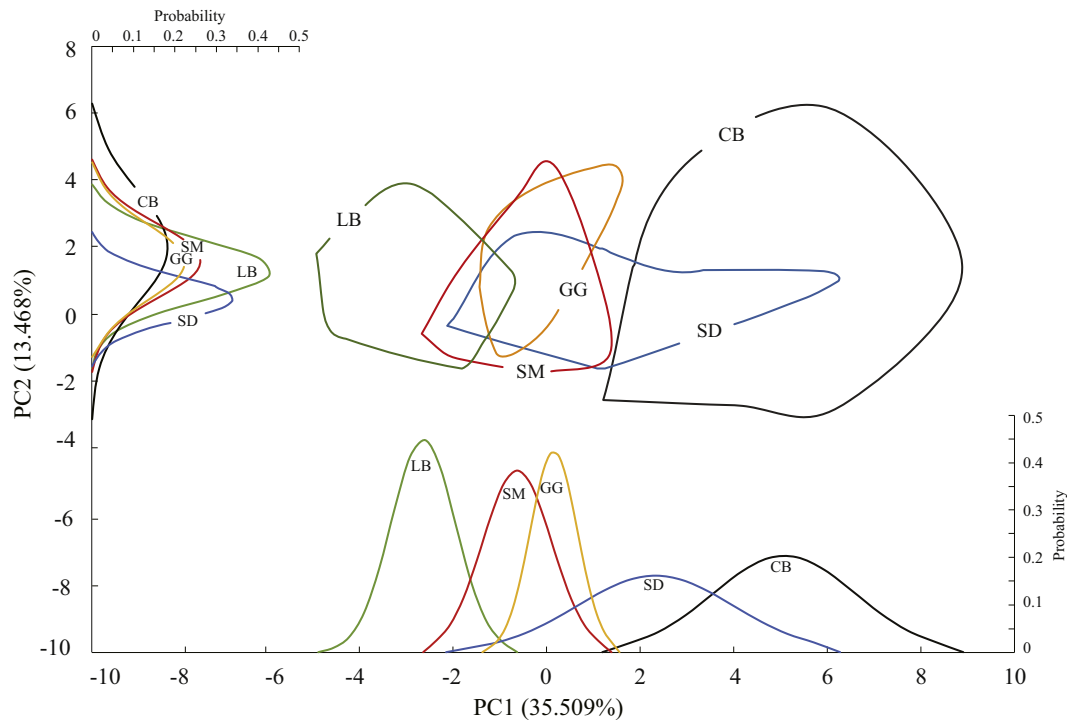
**Fig. 4.** Two dimensional ordinations of nesting habitat overlap among five bird species on the first two principal components. Contribution of variables to each component are summarized in the text (LB = light-vented bulbul, CB = Chinese blackbird, SM = scaly-breasted munia, SD = spotted dove, and GG = grey-capped greenfinch).

2017), including high human density (Kight and Swaddle, 2007), increased artificial light (Dominoni et al., 2013; Gaston et al., 2013), higher levels of chemical pollution (Bichet et al., 2013; Hui, 2002), elevated levels of noise (Fuller et al., 2007; Laiolo, 2010; Slabbekoorn and Ripmeester, 2008) and fewer areas of relatively natural habitat that provide the resources that most species require (Alberti et al., 2017; Grimm et al., 2008). Our survey indicated that most birds (93.66%) nested in the tree of artificial green belts (Fig. 1), which seems to be a better breeding habitat than other land types for urban birds. Compared to buildings and secondary forests, the artificial green belts could provide more nesting opportunities for birds. Although birds could derive more benefit from the abundant food in building than that in artificial green belts, the closer the birds are to the human environment, the more disturbance the birds receive, such as night lighting and noise from human activities. Meanwhile, secondary forests are farther from the human environment than artificial green belts, where birds receives less human interference, but food is not as readily available in artificial habitats (Morelli et al., 2014; Morgan et al., 2010; Sol et al., 2011). Both make buildings and secondary forests unsuitable for bird breeding. Contrarily, birds could benefit from the many resources that are available in green belts, including excess human food waste, fruits and flowers of ornamental plants (McKinney, 2006), and the protection that cities

**Table 3**
Nest site selection models ($\Delta AIC_C = 0$) of five bird species, the lowest $\Delta AIC_C$ model from each model subset.

| Species | Best model parameters | $AIC_C$ | $\Delta AIC_C$ | $w_i$ | K | AUC |
|---|---|---|---|---|---|---|
| LB | NSH + MSI + MSII+DR + DW | 323.033 | 0.000 | 0.708 | 6 | 0.959 |
| CB | NSH + GD + CC + MSI + MSII +DW | 104.886 | 0.000 | 0.331 | 6 | 0.973 |
| SM | GD + MSII+DR | 369.146 | 0.000 | 0.665 | 4 | 0.737 |
| SD | GD + PCC + MSI + MSII+DR | 162.306 | 0.000 | 0.542 | 6 | 0.779 |
| GG | NSH + GD + PCC + CC + MSI | 65.806 | 0.000 | 0.459 | 6 | 0.765 |

$AIC_C$ is Akaike's Information Criterion corrected for small sample size. $\Delta AIC_C$ is difference in $AIC_C$ relative to minimum $AIC_C$. $w_i$ is the Akaike model weight. K is number of parameters. AUC is the area under the receiver operating characteristic (ROC) curve. Variables descriptions are found in Table 1.
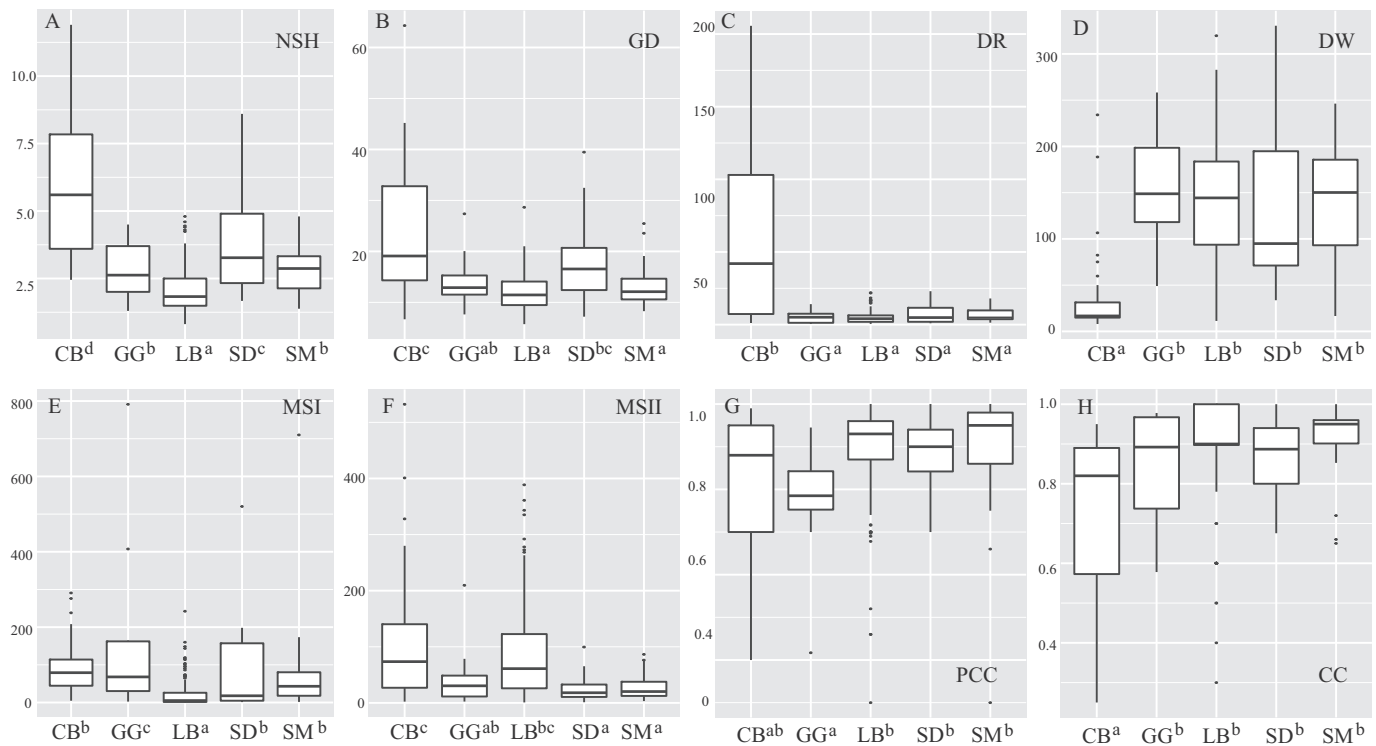
provide from other predators that cannot persist in urban environments, as well as relatively less disturbance from human being.

Birds' nest site selection was also affected by the life habit of predators in urban habitats. To avoid predation, many bird species have evolved adaptations of the nest-site choice (Martin, 1998, 1988). The different species selected nesting strategies to reduce the breeding loss from predators. The outcome of our work highlighted that birds nesting in trees with higher NSH or CC or lower DR were in favor of breeding success for various species, which could reduce the risk of predation when birds breed in green belts. First, the high nest site could reduce the possibility of being searched by the ground predator (including snakes and rodents), probably due to difficult accessibility (Rendell and Robertson, 1989). This explained our results from nest selection models, which indicated that the nest site of grey-capped greenfinches was positively correlated with NSH (Appendix Table E). Second, foliage next to the nest can reduce the probability of predation by concealing the nest (Martin, 1993), which was supported by our results that the nest site of the Chinese blackbird was positively correlated with CC (Appendix Table E). Third, bird nesting by the roadside is considered safe for breeding, because road traffic would discourage predators (Pescador and Peris, 2007), which was supported by the results that the nest site selections of light-vented bulbul, scaly-breasted munia and spotted dove were strongly negatively correlated with DR (Appendix Table E). In addition, as a new rapidly urbanizing and developing habitat for birds, alien predator may adapt to this urban environment with time lag, which makes raptors scarce in city (Barraquand and Nielsen, 2018; Sedinger et al., 2016). Therefore, birds could not benefit from the high values of PCC, which may be due to the presence of mainly ground predators and absence of aerial predators in this area, which is consistent with our analysis that the concealment factor, but not the percent of canopy, dominates the nest site selection.

### 4.2. Competition and coexistence of birds in urban environment

Competition among species can influence their distributions and utilization of environmental resources when birds nest in cities. Urban

**Fig. 5.** Mean ± SD of Best model parameters of five bird species (LB = light-vented bulbul, CB = Chinese blackbird, SM = scaly-breasted munia, SD = spotted dove, and GG = grey-capped greenfinch). Variables descriptions are found in Table 1.

habitats differ from rural and natural environments in the height of total vegetation cover, number of vegetation layers and fragmentation of wooded areas (Lowry et al., 2012; Sol et al., 2013). This competition broadly influences species responses to urbanization, particularly along gradients of environmental challenge (Martin and Bonier, 2018). Taking into consideration of our results, there is low competition between light-vented bulbul and Chinese blackbird, while the competition among scaly-breasted munia, spotted dove and grey-capped greenfinch seems to be intense (Fig. 4), but they are differentiation in the use of some characteristics (e.g., NSH, GD, MSI and PCC, see Fig. 5). The pressure of competition has led to various species of bird preferences for different environmental characteristics (Futuyma and Moreno, 1988; Martin and Bonier, 2018).

Coexistence can occur for two (or more) species in the overlapping distribution areas when niche divergence is present (Schoener, 1974; Tokeshi, 2009). Obviously, according to our findings, the niches of each species are different from those of others, which makes it possible to decrease the competition among them. If species prefer to coexist in the same distribution area, they must reduce their overlap (at least in one dimension) with the niche (Schoener, 1983). Vertically, the studied species differed in preferences related to the NSH and GD (Fig. 5A and B). Only scaly-breasted munias and grey-capped greenfinches preferred to nest in the tree with a similar NSH, and the other species nested in different NSHs. Chinese blackbirds and spotted doves liked to nest in a higher GD than did light-vented bulbuls, scaly-breasted munias and grey-capped greenfinches. Horizontally, Chinese blackbird was the farthest from the road, and there was no difference among the other birds (Fig. 5C). Conversely, Chinese blackbird was closest to water resources than were the other species (Fig. 5D). This is related to feeding habits; light-vented bulbul, scaly-breasted munia, spotted dove and grey-capped greenfinch are phytophagous, while Chinese blackbird is predominantly carnivorous (mainly including earthworms and insects) during the breeding season (Zhao, 2001). Nesting nearer to water sources and further from roads (more invertebrates) makes it easier for the Chinese blackbirds to get rich food (Cheng and Huang, 2012).

This niche differentiation adapting to urbanization in the long-term process, makes various birds live in harmony in urban area (Gause, 1934; Schoener, 1983, 1974; Tokeshi, 2009).

Birds keep a certain spacing between two nests during breeding, as it is conducive to reducing competition. Our results of nest selection models indicated that both the interspecific and intraspecific spacing of nests were critical for birds' nesting selection. Compared to light-vented bulbul, four other species maintained relatively large spacing in intraspecific nests (Fig. 5E), which means there is stiff competition between the intraspecific nests of light-vented bulbul. However, the nesting proximity between intraspecific species benefits breeders from the earlier detection of predators, group defense and the dilution of predation (Brown and Brown, 2001; Krause and Ruxton, 2002; Serrano et al., 2005), which is a trade-off of light-vented bulbul between intraspecific competition and the advantages of having adjacent nesting sites. For interspecific relationships, light-vented bulbul and Chinese blackbird had relatively larger nest spacing, which is beneficial to reducing intraspecific and interspecific competition (Futuyma and Moreno, 1988; Zheng, 1995). However, scaly-breasted munia, spotted dove and grey-capped greenfinch had relatively smaller spacing (Fig. 5F), which might be explained by species differentiation resources in the urban environment. The niche of these three species is different in other characteristics and the niche complementarity can lead to the utilization of aggregated resources (Zheng, 1995). However, competition between species might occur only if a resource that is required by both species is limited (Conner and Adkisson, 1977).

Urban green belts provide a suitable habitat for birds where various tree species mean a variety of options for nesting. Light-vented bulbuls and Chinese blackbirds nest on unique tree species, while scaly-breasted munias, spotted doves and grey-capped greenfinches do not show any nesting preferences to tree species (Fig. 2). This might because the degree of competition pressure leads to different coping strategies of birds. The result of PCA indicated that light-vented bulbuls and Chinese blackbirds suffered less pressure from interspecies competition, while scaly-breasted munias, spotted doves and grey-capped

greenfinches must receive higher pressure from interspecies competition, and then nest on various tree species to reduce competition. These differences among coexisting species in their use of space, is regularly observed and often thought to reflect the primary role of competition in determining the coexistence of species (Martin, 1988). When birds compete for shared resources at the same time, they can coexist if their consumption of one resource can be compensated by the others (Futuyma, 1983; Futuyma and Moreno, 1988; Sepp et al., 2018). Furthermore, bird preferences for nest tree species were also determined by the characteristics of local vegetation. *Camellia japonica* is the dominant species of low-lying trees, while *Cinnamomum camphora* is the main great tree in the artificial green belts in our study area, which is consistent with light-vented bulbul and Chinese blackbird nesting in *Camellia japonica* and *Cinnamomum camphora*, respectively. In Hangzhou, *Osmanthus fragrans* is one of the dominant tree species which is the main nesting tree species for light-vented bulbul (Lan et al., 2013; Wang et al., 2003). Because *Cinnamomum camphora* is scarce in Guiyang, Chinese Blackbird prefers to nest in the trunk of great trees including *Catalpa ovatum* and *Trachycarpus fortunci* (Wu and Li, 1984). The resource utilization of the species may be multidimensional, and species that overlap in one-dimensional spaces should have different characteristics in other dimensions (Zheng, 1995).

Birds have played an important role advancing study on the impact of urbanization. Economic development might accentuate the consequences of competitive interactions, thereby reducing local diversity in cities (Bozek et al., 2007; Cohen, 2006; Maher and Lott, 2000; Martin and Bonier, 2018). Within cities, the bird species density was highest in cities with the lowest proportion of urban land cover (Aronson et al., 2014), which indicated that the provision of green space at the city scale is crucial to bird species conservation in cities (Chace and Walsh, 2006; Evans et al., 2009). There are similar physical characteristics and environmental conditions in cities. Meanwhile, cities provide a distinctive opportunity to investigate the urban birds. However, there are few generalities of the patterns and drivers of urban birds and even fewer global comparative studies. Research on different environmental gradients is necessary for the study and protection of urban birds.

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