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# Exploring the relationship between frugivorous birds and fruit trees in urban parks using citizen science data

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**Abstract**
The occurrence of frugivorous bird species is strongly associated with the occurrence of fruit tree species in natural environments. However, the presence of a similar relationship in urban areas has not been explored. In this study, we used citizen science and field data to test for the existence of this relationship in 24 urban parks in Beijing, China. We compared the species richness and species composition of the two groups after accounting for park area, differences in diet among bird species, and differences in phenology between the two groups. We also constructed an interaction network between frugivorous bird and fruit tree species to evaluate the importance of each fruit tree species. Our results showed a significant positive relationship between the species richness of frugivorous birds and fruit trees. This relationship was significant year-long except during the summer for 133 bird-tree pairs. Park areas did not significantly affect the relationship. However, we found the interaction effect of the park area and the richness of fruit tree species mediated the relationship in certain months. We did not detect significant relationships in species composition between frugivorous birds and fruit trees. Amur honeysuckle (*Lonicera maackii*), Chinese Juniper (*Sabina chinensis*), and Oriental persimmon (*Diospyros kaki*) played a central role in the network of frugivorous bird and fruit tree species. Our results provide evidence for cross-trophic interactions between frugivorous bird species and fruit tree species, justifying planting fruit trees to enhance bird diversity and resilience in urban areas. However, this objective should focus on maximizing fruit production by planting key fruit tree species rather than increasing the total number of fruit tree species.

**Keywords** Frugivorous birds · Fruit trees · Inter-species interaction · Urban green space

## Introduction

Urban birds are an important component of urban biodiversity. Due to their wide distributions and sensitivity to environment change, birds also serve as a critical indicator of the status of urban biodiversity (Koskimies 1989; Fraixedas et al. 2020). Urbanization have been found to impact bird diversity negatively. Decreasing species richness, phylogenetic, and functional diversity have been observed globally for birds in urban areas (Sol et al. 2017, 2020; La Sorte et al. 2018; Marcacci et al. 2021; Sidemo-Holm et al. 2022). It is therefore imperative to take action that will slow or even reverse these negative trends. To achieve that goal, we need robust information on how urban environments affect different aspects of bird diversity.

Bird diversity is affected by many factors in urban environments. This includes food availability, which is a vital component (Galbraith et al. 2015; He et al. 2021; Yin et al. 2023). The availability of food sources in urban

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environments determines the species richness and density of birds (Ciach and Fröhlich 2017). A lack of specific food resources has led to the dominance of generalist species in urban bird communities (Patankar et al. 2021). Besides general availability, the types and quality of food resources, the synchrony with bird occurrences, and nature of the interactions between birds and these resources affect how birds use food resources. Khan et al. (2023) found that foraging of Chinese fan palm (*Livistona chinensis*) berries by two common urban birds peaked in December and January when no other fruits were available in the urban landscape. Palacio and Montalti (2023) found significant trait matching between functional traits of birds and alien invasive plants. Shanahan et al. (2011) showed that bird foraging height preferences are a good predictor of bird abundance in response to woody vegetation structure. All those examples show that understanding the patterns and associations between food resources and urban bird communities is essential to comprehend urban bird biodiversity.

Plant fruits are an important food source for birds due to their abundant nutrients such as sugars and lipids (Blendinger et al. 2015). The reliance on fruits is the most obvious among frugivorous birds. Consequently, a strong correlation between the richness of frugivorous birds and the species richness of fruit trees or fruit abundance has been observed in natural environments. Kissling et al. (2007) found that the richness of Ficus tree species in sub-Saharan Africa had the strongest direct effect on the richness of frugivorous bird species. Ferger et al. (2014) quantified the effects of fruit abundance on the species richness of 19 frugivorous bird species in Tanzania and found they were positively associated. The relationship between frugivorous birds and fruits can shape the species composition of birds and vice versa. A study showed that the traits of fruits and birds determined the species composition of the tree and bird communities on the Hawaiian Islands (Case and Tarwater 2020). Whether the same relationship exists between frugivorous birds and fruit trees in urban areas is still unclear. If the relationships found in natural environments are replicated in urban environments, specific fruit trees can be planted in cities to increase the diversity of frugivorous birds.

To our knowledge, this question has not been addressed. However, many studies have observed the consumption of fruits by urban birds, which suggests the existence of such relationships. A general positive relationship between urban bird richness and fruit tree richness have been observed in many parts of the world, including Nanjing, China (Zhang et al. 2022a), Salvador, Brazil (Andrade et al. 2011), and Buenos Aires, Argentina (Zietsman et al. 2019). Also, the association between the species richness of urban birds and fruit tree was stronger in winter and early spring when other food sources are scarce (Yong et al. 2014; Zhang et al. 2022a; Yin et al. 2023). Some species-specific relationships have also been documented. For example, Luchu juniper (*Juniperus taxifolia*) is an important food source for Light-vented Bulbul (*Pycnonotus sinensis*) in the winter and early spring (He et al. 2021). While these findings point to possible relationships between frugivorous birds and fruit tree species, conclusive evidence is missing due to several issues. First, existing studies mainly focused on the relationship between the species richness of urban birds and fruit trees (Shi et al. 2016; Kim et al. 2016; Peng et al. 2020). The species composition of the two communities as well as inter-species interactions are rarely considered (Kissling et al. 2007; Li et al. 2022; Wang et al. 2023). Second, existing studies often used qualitative descriptions rather than quantitative analysis (He et al. 2021; Zhang et al. 2022a). Qualitative descriptions alone are insufficient to prove the robustness of the observed patterns. Finally, due to the high demand for labor and resources in field observations of birds, many studies are based on short-term observations conducted during a single season or year (Tan and Yang 2010; Yang et al. 2015a; Yin et al. 2023). Short-term observations can be haphazard, increasing uncertainty in the results and conclusions.

With the above limitations in mind, this study aims to address the research question: Can significant inter-species relationships between frugivorous bird species and fruit tree species be identified in urban areas? To answer this question, we take advantage of citizen science data. Citizen science initiatives can provide long-term bird occurrence data across broad geographic regions. Its value in studying urban birds has been well tested (Duan and Li 2020; Lepczyk and Vargo 2023; Wang et al. 2024; La Sorte et al. 2023), including their diets (Sandvig and Cerpa 2022; Appel and de Oliveira Porfirio 2023). We chose Beijing, China, as our study site due to the city's leading position in citizen science. Beijing has a large and dedicated birdwatching community. Just in 2022, 1,275 birdwatching reports were submitted by bird watchers, encompassing observations of 392 avian species (Suzaku Ornithology Institute 2022). Our study addresses the following two objectives: (1) to detect the relationships between frugivorous bird species and fruit tree species in urban areas, and (2) to analyze their interspecific associations at the species and community levels.

## Methods

### Study area

Beijing, China (115°42 '~ 117°24' E, 39°24 '~ 41°36' N) is located in the warm temperate sub-humid region (Zhao 2019). Beijing has an extensive urban green space system. By the end of 2022, the green space area in Beijing had reached 93,558 ha, with a per capita green space area of 42.85 m$^2$. A total of 1,050 parks have been built in the city. Beijing has a high bird diversity. Around 503 bird species have been recorded in Beijing by 2021, accounting for about one-third of the total recorded bird species in China (Beijing Municipal Forestry and Parks Bureau 2021).

We selected 24 parks from 573 parks in the six urban districts of Beijing as our study sites (Fig. 1). To support the representativeness of the selected park, the 573 parks were first classified into 24 groups according to their size, establishment date, and the surrounding land cover. The size classes include small (< 10 ha), medium (> 10 ha and < 20 ha), and large (> 20 ha). Establishment date includes two classes, before and after 2000. Three land cover classes, impervious surface, vegetation, and water surface were summarized within a 1.5 km buffer around each park. Each park was classified into six categories after controlling for the surrounding environment conditions: small parks established before and after 2000, medium parks established before and after 2000, and large parks established before and after 2000. The sizes and establishment times of the 24 parks were collected from the Beijing park management agency (Beijing Municipal Forestry and Parks Bureau 2022a). The impervious surface area, green space area, and water area in each park's 1.5 km buffer zone were derived using Beijing's land cover data extracted from the PKU Urbanscape Essential Dataset (Zhang et al. 2022b).

## Data collection

Tree species that could serve as potential avian food resources were surveyed in the 24 parks in August 2022. Before conducting the field survey, a list of tree species that are potential food resource for birds was compiled from the literature and expert opinions (Sui et al. 2006; Tan and Yang 2010; Wang et al. 2016; Lu and Lu 2019; Zhao 2019; He et al. 2021; Yin et al. 2023). Each park was divided into multiple zones according to their sizes and the distribution of green spaces. Volunteers, primarily undergraduate and graduate students majoring in landscape architecture and forestry, were allocated to different zones. Each volunteer then compiled information on species composition, abundance, life form (liana, tree, and shrub), vertical height, diameter at breast height (DBH) of trees or base diameter of shrubs. Bird occurrence records from November 2019 to November 2022 were obtained from the citizen science projects eBird (www.ebird.org) and China Bird Report (www.birdreport.cn). The bird occurred data were screened using the following filters. Only complete records complied with standard observation time and distance were selected for analysis. The observation time was from 5 to 240 min and the distance surveyed was less than 10 km, following La Sorte and Somveille (2020). The bird taxonomy was based on the International Ornithological Congress World Bird List (Gill et al. 2020).

Although mainly tree species with fleshy fruits are examined with frugivorous birds (Şekercioğlu et al. 2004), in this study, we define 'fruit trees' as all fruit-bearing trees,

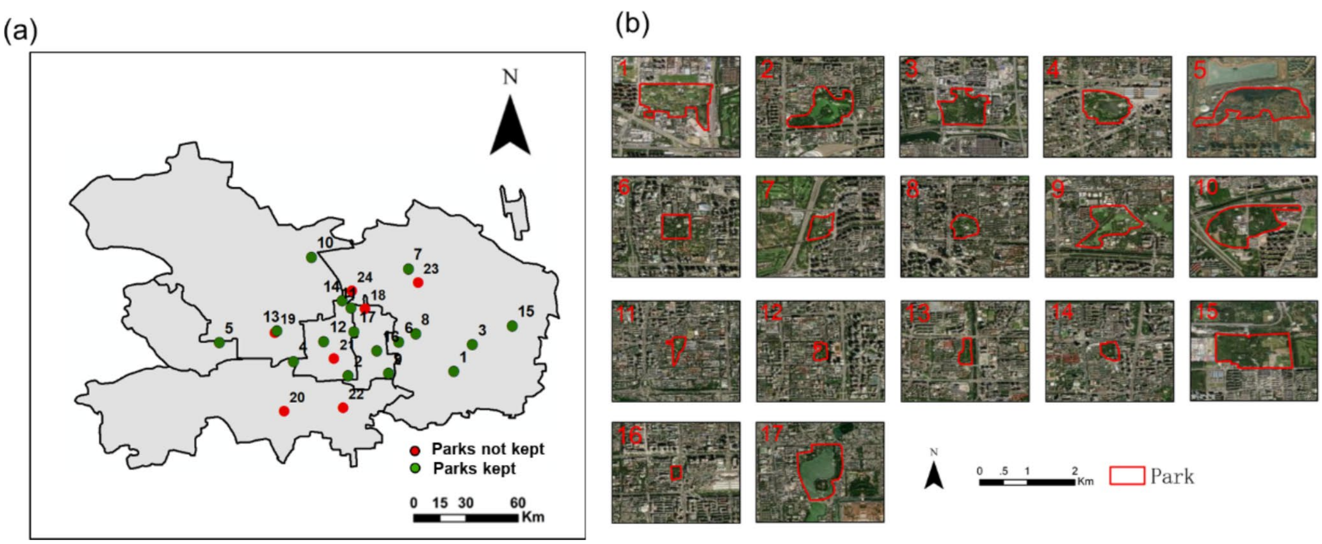


**Fig. 1** The study sites. (**a**) Distribution of the 24 parks in Beijing's six urban districts, (**b**) Satellite images of the 17 parks retained for analysis: 1. Guanzhuang Park; 2. Taoranting Park; 3. Xinglong Park; 4. Lianhuachi Park; 5. Laoshan City Leisure Park; 6. Ritan Park; 7. Beihe Park; 8. Tuanjiehu Park; 9. Longtan West Lake Park; 10. Dongsheng Palka Country Park; 11. Rending Lake Park; 12. Moon Temple Park; 13. Linglong Park; 14. Shuangxiu Park; 15. Changying Park; 16. Dongdan Park; 17. Beihai Park; 18. Ande City Forest Park; 19. Dinghui Park; 20. Fengtai Science and Technology Park; 21. Quang Ninh Park; 22. Huai Sun Country Park; 23. Jinyu Nanhu Park; 24. Madian Park

provided they serve as avian food resource. Correspondingly, we define 'frugivorous birds' as bird species that consume fruits from these tree species. These broader definitions align with the dietary needs of urban birds in Beijing, especially during winter when dry fruits are crucial for survival (He et al. 2021; Yin et al. 2023). Including diverse fruit types when studying frugivorous birds have also been adopted in other studies (Foster 1977; Galindo-González et al. 2000; Lim and Sodhi 2004).

## Data analysis

We adopted the following steps to address limitations in our data. First, we selected parks that contained relatively complete bird occurrence records. Second, instead of lumping all bird species together, we divided them into guilds based on their reliance on specific fruits as food resources. Third, we considered phenological matching between the timing of fruit occurrence and frugivore bird occurrence.

To avoid biases introduced by incomplete bird occurrence records, we used the sample coverage of rarefied samples to estimate the completeness of the bird occurrence data compiled in each park (Hsieh et al. 2016). Sample coverages higher than 90% was considered complete in this study, resulting in the retention of 17 parks for analysis.

We classified the bird species into four guilds (Kissling et al. 2007, 2009; Wilman et al. 2014; Wang et al. 2021). The four guilds are defined as: (1) obligate frugivores; (2) partial frugivores (other food items represent major components of their diet, e.g., terrestrial invertebrates); (3) opportunistic frugivores (occasionally supplement their diet with fruits), and (4) non-frugivores. Only obligate and partial frugivores were considered in our analysis because of their strong reliance on fruits as a food resource.

To reveal the true interactions between frugivorous birds and fruit trees, we constructed an interaction table between trophic levels through phenological matching. A tree species' fruiting time was determined by consulting *The Flora of China* (Li 2007) and local experts. The time of occurrence of bird species in Beijing were obtained from *Common Wild Birds Guide – Beijing Area* (Li 2014). If the fruiting time of a tree species overlapped with the occurrence time of a bird species in Beijing, we considered that there was a possibility that the two species could interact. We further separated the realized interactions from potential interactions if the interactions were observed in the field as well as compiled from photos (Fig. 2), videos, or birding notes obtained through searching the internet.

To examine the relationship between the species richness of frugivorous birds and fruit trees, we fit univariate regression models with species richness of frugivorous birds in each park as the response variable, and the species richness of fruit trees as the explanatory variable. The same analysis was repeated for each month by considering phenological matching. For comparison, we also ran univariate regression models using the species richness of all birds as the response variable and the species richness of fruit trees as the explanatory variable.

To determine the effect of park area on the relationship between the richness of fruit trees and frugivorous birds, we fit multivariate regression models using the species richness of frugivorous birds in each park as the response variable and the species richness of fruit trees and the park area as the explanatory variables. The same analysis was repeated for each month by considering the phenological matching. Then, we added the interaction term of fruit tree richness and the park area as another explanatory variable in the multi-regression model to further explore how their combined effects influence this relationship.

We used the Mantel test to analyze the correlation between the community composition of frugivorous birds and the fruit tree communities. The Mantel test is frequently used to test the correlation between two matrices (Legendre and Fortin 2010). We used the bird occurrence data to generate the dissimilarity matrix for frugivorous birds in the 17 parks. For fruit tree species, both the occurrence data and the relative abundance data were used to calculate the dissimilarity matrices. It is known that the values of occurrence-based indices are constantly higher than abundance-based indices (Yang et al. 2015b). Because the bird abundance estimates from citizen-science initiatives are generally considered unreliable (Robinson et al. 2021), we did not use them in our analysis. The Simpson dissimilarity index was calculated for occurrence data, while the Bray-Curtis distance was calculated for the relative abundance data of fruit tree species. We used the Spearman correlation coefficient in the Mantel tests, and we set the number of permutations to 9999. The above analysis was carried out at both annual and monthly scales.

To detect significant co-occurrence between frugivorous bird species and fruit tree species, we ran a species co-occurrence analysis following the method developed by Veech (2013). The entire interaction table was first divided into 12 small tables by month. We then arranged the frugivorous birds and fruit trees into a presence-absence matrix for each park. Pairwise null model analysis was applied to the presence-absence matrix to determine whether species pairs had significant co-occurrences. We used the probabilistic modeling approach to calculate the expected frequency of co-occurrence between each species pair based on the assumption that the distribution of one species is independent of the second species (Fois et al. 2022). The expected frequency was compared to the observed frequency and the probability that a lower or higher value of co-occurrence


**Fig. 2** Examples of birds feeding on tree fruits. (**a**) Light-vented Bulbul - Amur honeysuckle (*Lonicera maackii*), (**b**) Light-vented Bulbul - Chinese Juniper (*Sabina chinensis*), (**c**) Bohemian waxwing (*Bombycilla garrulus*) & Japanese waxwing (*Bombycilla japonica*) - Asiatic apple (*Malus spectabilis*), (**d**) Japanese waxwing - Amur honeysuckle. Photos taken by Xinyi Liu

could have been obtained by chance was returned. The results include a probability of co-occurrence, which can be interpreted as a *p*-value. In this study, significant probabilities of co-occurrence were retained upon a threshold of $p<0.05$. The species co-occurrence analysis was run for both potential interactions and realized interactions.

To assess the importance of individual fruit tree species, we built networks between frugivorous bird species and fruit tree species. We calculated three network indices: (1) species degree, which is the sum of links per species; (2) resource range, which measures the extent to which resources are utilized, with a value of 0 when all resources are used and 1 when only one resource is used, and (3) species specificity, which measures the variability of interactions, normalized between 0 and 1, with lower values suggesting low specificity and higher values indicating higher specificity in species interactions. Again, species involved in both potential interactions and realized interactions were analyzed.

All analysis and data visualizations were conducted in the R software environment for statistical computing and graphics, v.4.2.1 (R Core Team 2024). The rarefaction curve was calculated using the R package iNEXT (Hsieh et al. 2016). The BAT R package was used to generate the dissimilarity matrices and run the Mantel tests (Cardoso et al. 2015). The species co-occurrence analysis was implemented using the Cooccur R package (Griffith et al. 2016). The network analysis was implemented using the Bipartite R package (Dormann 2011).

# Results

## Bird and tree occurrence data

A total of 182 plant species from 77 families were recorded across the 17 parks, averaging 48 species per park (SD = 19). From these, 124 were tree species, 52 were shrub species, and 6 were vine species. The most common tree species were Chinese scholar tree (*Styphnolobium japonicum*), Siberian elm (*Ulmus pumila*), and Chinese juniper (*Sabina chinensis*). A total of 13,728 bird occurrence records were collected, of which 10,718 were retained after cleaning. A total of 114 bird species were documented, averaging 41 species per park (SD = 25). The most common bird species included the Eurasian tree sparrow (*Passer montanus*), Azure-winged magpie (*Cyanopica cyanus*), and Oriental magpies (*Pica serica*). From the 114 bird species, four were classified as obligate frugivores, 33 as partial frugivores, 28 as opportunistic frugivores, and 49 as non-frugivores (Table S1).

## The feeding relationship between frugivorous birds and fruit trees

Based on phenological matches between frugivorous birds and fruit trees, we obtained a table of interactions between the two communities. The table includes 37 frugivorous bird species, 53 fruit tree species, and 1,809 potential interactions (Table S2). Among the potential interactions, 133 were realized interactions, involving 28 fruit tree species and 24 frugivorous bird species. The phenological matching results between fruit tree species and four obligate frugivore species in 17 parks are presented in Table 1.

## The associations between the species richness of frugivorous birds and fruit trees

At the annual scale, a positive but insignificant relationship existed between the species richness of all birds and fruit trees ($R^2 = 0.18$, $p = 0.062$). The same relationships were observed between the richness of frugivorous birds and fruit trees for potential and realized interactions ($R^2 = 0.15$, $p = 0.069$; $R^2 = 0.15$, $p = 0.067$). On the monthly scale with potential interactions, there were significant positive associations between the species richness of frugivorous birds and fruit trees during February, November, and December (Fig. 3). On the monthly scale for realized interactions, there were significant positive relationships between the species richness of frugivorous birds and fruit trees during all months except for April, May, June, and July.

After adding the park area as a covariate in the regression model, no significant relationship among the richness of frugivorous bird species, the richness of fruit tree species, and the park area at annual or monthly scales for bird-tree pairs with potential interactions were detected (Table S9). For realized interactions, there was a significant positive relationship between the richness of frugivorous bird species and the richness of fruit tree species in January, February, September, and October even when the park area was considered, while there was no significant relationship between richness of frugivorous bird species and the park area (Table S10). Furthermore, the interaction effect between the richness of fruit tree species and the park area was significant in March, August, November, and December for bird-tree pairs with realized interactions (Table 2).

## The associations between the species compositions of frugivorous birds and fruit trees

The Mantel test (Table S3-S8) showed no significant correlations between the frugivorous bird and fruit tree species assemblages in the 17 parks, regardless of whether presence-absence data or relative abundance data were used at annual or monthly scales (Table 3).

Three species pairs showed significant positive co-occurrence and one pair showed significant negative co-occurrence when considering all potential pairwise interactions (Fig. 4a). If only realized interactions were considered, two species pairs displayed significant positive co-occurrence (Fig. 4b).

## Critical species from the frugivorous bird - fruit tree network analysis

Three fruit tree species, Amur honeysuckle (*Lonicera maackii*), Chinese Juniper (*Sabina chinensis*), and Oriental persimmon (*Diospyros kaki*), interacted with most frugivorous bird species (Fig. 5). The three fruits trees species had species degree values of 19, 12, and 11, respectively. The three fruit tree species also had the lowest resource range (0.22, 0.52, 0.57) and species specificity (0.11, 0.21, 0.23) values, respectively (Table 4).

# Discussion

This study found a significant positive relationship between the species richness of frugivorous birds and fruit trees at the monthly scale. The relationship was significant except during the summer based on their realized interactions.

**Table 1** The phenological matching results between fruit trees and four obligate frugivores in 17 parks

| Tree species | | Obligate frugivores | | | |
|---|---|---|---|---|---|
| Common name | Scientific name | Light-vented bulbul *(Pycnonotus sinensis)* | Black-naped Oriole *(Oriolus chinensis)* | Bohemian waxwing *(Bombycilla garrulus)* | Japanese waxwing *(Bombycilla japonica)* |
| Chinese Thuja | *Platycladus orientalis* | **1 2 3 4 5 6 7 8 9 10 11 12** | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Luchu juniper | *Juniperus taxifolia* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese Juniper | *Sabina chinensis* | **1 2 3 4 5 6 7 8 9 10 11 12** | 5 6 7 8 9 | **1 2 3 4 11 12** | **1 2 3 4 11 12** |
| Black locust | *Robinia pseudoacacia* | **1 2 3 4 5 6 7 8 9 10 11 12** | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Persian silk tree | *Albizia julibrissin* | 8 9 10 | 8 9 | NA | NA |
| Japanese pagoda tree | *Sophora japonica* | **1 2 3 4 5 6 7 8 9 10 11 12** | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese scholar tree | *Styphnolobium japonicum 'Pendula'* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese redbud | *Cercis chinensis* | 8 9 10 | 8 9 | NA | NA |
| Hardy rubber tree | *Eucommia ulmoides* | 4 5 | 5 | 4 | 4 |
| Japanese Yew | *Taxus cuspidata* | 8 9 | 8 9 | NA | NA |
| Common Walnut | *Juglans regia* | 10 11 12 | NA | 11 12 | 11 12 |
| Yulan Magnolia | *Magnolia denudata* | **8 9 10** | 8 9 | NA | NA |
| Japanese tree lilac | *Syringa reticulata* | 9 10 | 9 | NA | NA |
| Green Ash | *Fraxinus pennsylvanica* | **1 2 3 8 9 10 11 12** | 8 9 | 1 2 3 11 12 | 1 2 3 11 12 |
| Chinese privet | *Ligustrum lucidum* | **1 2 3 4 5 7 8 9 10 11 12** | 5 7 8 9ś | 1 2 3 4 11 12 | **1 2 3 4 11 12** |
| Chinese ash | *Fraxinus chinensis* | 8 9 10 11 12 | 8 9 | 11 12 | 11 12 |
| Smoketree | *Cotinus coggygria* | 5 6 7 8 9 | 5 6 7 8 9 | NA | NA |
| Shangtung maple | *Acer truncatum* | 8 | 8 | NA | NA |
| Hall crabapple | *Malus halliana* | 9 10 | 9 | NA | NA |
| Birchleaf pear | *Pyrus betulifolia* | 8 9 | 8 9 | NA | NA |
| Asiatic apple | *Malus spectabilis* | 1 2 3 8 9 10 11 12 | 8 9 | **1 2 3 11 12** | 1 2 3 11 12 |
| Catalpa tree | *Sorbus pohuashanensis* | 9 10 | 9 | NA | NA |
| Chinese plum | *Prunus salicina* | **7 8 9 10 11** | 7 8 9 | 11 | 11 |
| Downy cherry | *Prunus tomentosa* | **5 6** | 5 6 | NA | NA |
| Apple tree | *Malus pumila* | 7 8 9 10 | 7 8 9 | NA | NA |
| Ussurian pear | *Pyrus ussuriensis* | 8 9 10 | 8 9 | NA | NA |
| Plumleaf crab apple | *Malus prunifolia* | 1 2 3 8 9 10 11 12 | 8 9 | 1 2 3 11 12 | 1 2 3 11 12 |
| Siberian crabapple | *Malus baccata* | 9 10 11 12 | 9 | **11 12** | 11 12 |
| Chinese wild peach | *Prunus davidiana* | 6 7 8 | 6 7 8 | NA | NA |
| Siberian apricot | *Prunus sibirica* | 6 7 | 6 7 | NA | NA |
| Mountain hawthorn | *Crataegus pinnatifida* | **2 3 4 5 6 7 8 9** | 5 6 7 8 9 | 2 3 4 | 2 3 4 |
| Chinese photinia | *Photinia serratifolia* | 10 | NA | NA | NA |
| Midget crab apple | *Malus kaido* | **8 9** | 8 9 | NA | NA |
| Ansu apricot | *Armeniaca vulgaris* | **6 7** | 6 7 | NA | NA |
| Radiant crabapple | *Malus 'Radiant'* | 6 7 8 9 10 11 | 6 7 8 9 | 11 | 11 |
| Flowering almond | *Amygdalus triloba* | **5 6 7 8 9** | 5 6 7 8 9 | NA | NA |
| Cherry plum | *Prunus cerasifera* | 8 9 10 | 8 9 | NA | NA |
| Amur honeysuckle | *Lonicera maackii* | **8 9 10 11 12** | 8 9 | **11 12** | **11 12** |
| Paper mulberry | *Broussonetia papyrifera* | **6 7** | 6 7 | NA | NA |
| White mulberry | *Morus alba* | **5 6 7 8** | 5 6 7 8 | NA | NA |
| Dawn redwood | *Metasequoia glyptostroboides* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Pomegranate | *Punica granatum* | **9** | 9 | NA | NA |
| Date-plum | *Diospyros lotus* | 10 11 | NA | 11 | 11 |
| Oriental persimmon | *Diospyros kaki* | **9 10 11 12** | 9 | **11 12** | 11 12 |
| Common jujube | *Ziziphus jujuba* | 8 9 10 11 | 8 9 | 11 | 11 |
| lacebark pine | *Pinus bungeana* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese White Pine | *Pinus armandii* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Deodar cedar | *Cedrus deodara* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese red pine | *Pinus tabuliformis* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |

**Table 1** (continued)

| Tree species | | Obligate frugivores | | | |
|---|---|---|---|---|---|
| Common name | Scientific name | Light-vented bulbul *(Pycnonotus sinensis)* | Black-naped Oriole *(Oriolus chinensis)* | Bohemian waxwing *(Bombycilla garrulus)* | Japanese waxwing *(Bombycilla japonica)* |
| Golden Raintree | *Koelreuteria paniculata* | 1 2 3 4 5 6 7 8 9 10 11 12 | 5 6 7 8 9 | 1 2 3 4 11 12 | 1 2 3 4 11 12 |
| Chinese parasol tree | *Firmiana platanifolia* | 9 10 | 9 | NA | NA |
| Ginkgo biloba | *Ginkgo biloba* | 1 2 9 10 11 12 | 9 | 1 2 11 12 | 1 2 11 12 |
| Siberian elm | *Ulmus pumila* | **3 4** | NA | 3 4 | 3 4 |

Note: The number refers to the month the species pair interacts. NA refers to no matching months. Realized interactions are highlighted in green

Because summer is the breeding season for birds, birds tend to eat food with abundant protein, such as insects (Zuckerberg et al. 2016). At the same time, only a few tree species in Beijing produce fruits during the summer. Therefore, fruits are not the primary food source for urban birds during the summer. In contrast, birds rely more on fruits as a food resource during the fall and winter. The significant positive relationship between the species richness of frugivorous birds and fruit trees corroborates findings from other studies where fruiting plants have been identified as a crucial food resource for urban bird species (Pithon et al. 2021; Khan et al. 2023). The seasonal patterns of urban birds foraging on the fruit trees identified in our study agree with these documented by He et al. (2021) and Yin et al. (2023). However, in contrast to their qualitative findings, we found that these relationships were insignificant at the annual scale based on a quantitative analysis. Only after considering the phenology matching between the frugivorous birds and the fruit tree species were significant relationship revealed during specific months. Our findings demonstrate the importance of fruit tree species in urban areas to frugivorous birds.

Richness of fruit tree species was significantly associated with richness of frugivorous bird species, but the effect of park area mediated the relationship for specific months. The park area is a key determinant of bird species richness in urban parks through the influence of the ubiquitous species-area relationship (Lomolino 2000; La Sorte et al. 2020a). Our results corroborate this observation. However, during months with limited avian food sources, the influence of park area on the relationship between birds and fruit trees tends to be less pronounced. Fruits are the primary food source for urban birds in winter. He et al. (2021) found that in January and February, the fruits of garden plants were the main component of urban bird diets. Khan et al. (2023) found that foraging of Chinese fan palm (*Livistona chinensis*) berries peaked in January. Our results also showed that even when the park area was considered, a significant relationship between richness of frugivorous bird species and richness of fruit tree species still held. During periods when food sources are less limited, the relationships are impacted by the combined effect of the richness of fruit tree species and the park area.

We found no significant correlation between the community composition of frugivorous bird species and fruit tree species. The lack of significant correlation indicates that species-to-species specificity between frugivorous bird and fruit tree species is absent. Fruit morphological traits are often the restricting factor for fruit–frugivore interactions (Dehling et al. 2016; Gómez and Lois-Milevicich 2021; Peña et al. 2023). However, the fruits of the most popular fruit trees (Amur honeysuckle, Chinese Juniper, and Oriental persimmon) in Beijing are either small or soft. Various frugivorous bird species can eat them without restrictions. Therefore, the fruits of one tree species can be consumed by multiple bird species. Similar phenomenon has been observed in Singapore, where the species richness of birds feeding on strangler figs (*Ficus aurea*) was 4.5 times higher than those feeding on other species but the species composition between the two group was not significantly different (Chong et al. 2020). The lack of a species-to-species relationship can also result from homogenization of urban frugivorous birds and fruit tree communities driven by urbanization. The environment filter and human selection pressures homogenize urban bird and plant species, weakening the natural biological connection across trophic levels (Williams et al. 2015; Hensley et al. 2019). The above reasons may explain the lack of a strong association between the species composition of frugivore bird and fruit tree species. Similar findings have been observed in other ecosystems. For example, Fargeot et al. (2023) found no co-variation of biodiversity across trophic levels at the community level in a riverine freshwater ecosystem.

We identified four bird-tree species pairs displaying significant co-occurrence patterns, with three pairs showing positive and one negative. At small spatial scales, animal species are spatially associated with their food resources (Novotny et al. 2006). However, the number of positive co-occurrence species pairs is much less than those indicated by the realized interactions in our study area. One reason can be the lack of species-specific interactions between frugivorous birds and fruit trees in urban environments,

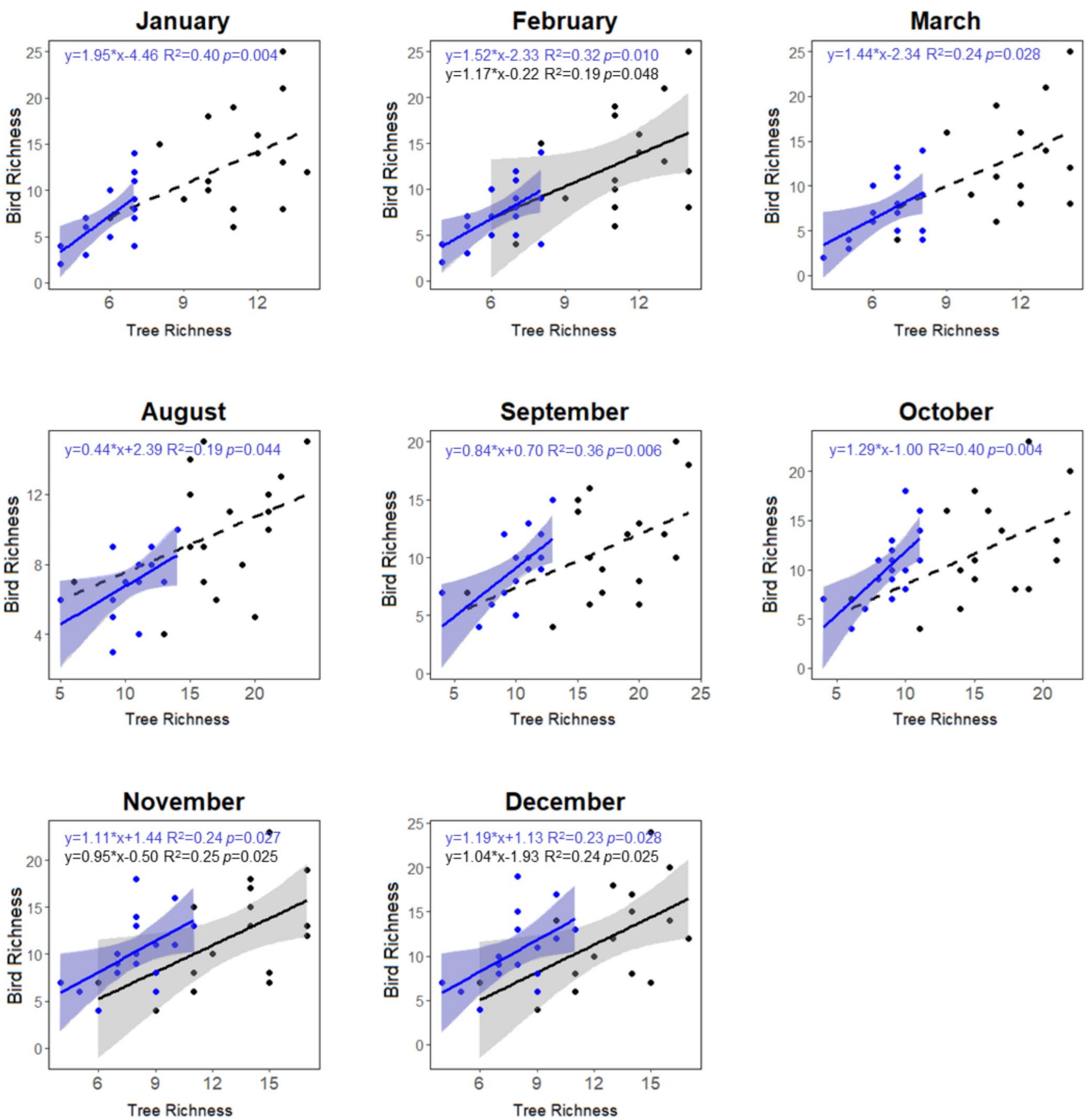


**Fig. 3** The relationship between the species richness of frugivorous birds and fruit trees during each month in 17 parks in Beijing, China. Blue points and lines represent realized interactions, and black points and lines represent potential interactions. Only significant results ($p < 0.05$) are shown

where the fruits of a single tree species may be consumed by multiple bird species. Another possible reason is the observation bias of citizen science data. The variations in species detectability and unbalanced preference for different species could influence the accuracy and completeness of the bird occurrence records, thus affecting the accuracy of the species occurrence data (Isaac et al. 2014; Fink et al. 2020; Johnston et al. 2021). For the three positive species pairs, both bird species and tree species were recorded in most parks. For the negative species pair, the tree species (Chinese redbud) was recorded in only 2 of the 15 parks where Light-vented bulbul was recorded. Co-occurrence analysis has been used to detect competitive or mutual interactions among species in natural habitats (Brazeau and Schamp 2019; Fois et al. 2022). Our finding suggests that further studies need to be conducted to test the possible

**Table 2** The results of regressing frugivorous bird richness against fruit tree richness and park area for bird-plant pairs with realized interactions. The interaction effect of fruit tree richness and the park area was included. Asterisk represents $p < 0.05$

| Time | Model fit | | Fruit tree richness | | Park area | | Fruit tree richness : Park area | |
|---|---|---|---|---|---|---|---|---|
| | $R^2$ | *p* value | Coefficient | *p* value | Coefficient | *p* value | Coefficient | *p* value |
| Annual | 0.347 | 0.651 | 0.317 | 0.551 | 0.215 | 0.512 | 0.005 | 0.693 |
| January | 0.445 | 0.047* | 2.405 | 0.043* | 0.142 | 0.690 | 0.022 | 0.667 |
| February | 0.400 | 0.046* | 1.802 | 0.039* | 0.178 | 0.384 | 0.024 | 0.396 |
| March | 0.387 | 0.036* | 1.524 | 0.139 | 0.321 | 0.196 | 0.039 | 0.032* |
| April | 0.334 | 0.140 | 1.058 | 0.355 | 0.282 | 0.190 | 0.037 | 0.257 |
| May | 0.279 | 0.220 | 0.491 | 0.550 | 0.078 | 0.560 | 0.006 | 0.755 |
| June | 0.268 | 0.241 | 0.268 | 0.572 | 0.156 | 0.182 | 0.015 | 0.284 |
| July | 0.257 | 0.262 | 0.317 | 0.441 | 0.118 | 0.205 | 0.012 | 0.294 |
| August | 0.310 | 0.012* | 0.166 | 0.653 | 0.129 | 0.323 | 0.012 | 0.047* |
| September | 0.531 | 0.017* | 0.449 | 0.029* | 0.283 | 0.091 | 0.026 | 0.083 |
| October | 0.454 | 0.043* | 0.999 | 0.045* | 0.105 | 0.620 | 0.012 | 0.580 |
| November | 0.347 | 0.025* | 1.325 | 0.170 | 0.195 | 0.293 | 0.020 | 0.028* |
| December | 0.343 | 0.029* | 1.430 | 0.172 | 0.185 | 0.304 | 0.019 | 0.049* |

**Table 3** The Mantel test results for the frugivorous bird and fruit tree species pairs. The Mantel test statistic (*r*) and *p*-values (shown in parenthesis) are presented at the annual and monthly scales for potential and realized interactions

| Time | Bird occurrence-tree occurrence data | | Bird occurrence-tree abundance data | |
|---|---|---|---|---|
| | Potential interactions | Realized interactions | Potential interactions | Realized interactions |
| Annual | 0.005 (0.467) | -0.164 (0.891) | 0.136(0.217) | 0.105 (0.235) |
| January | -0.134 (0.807) | -0.167 (0.873) | 0.071(0.329) | 0.056 (0.348) |
| February | -0.103 (0.747) | -0.153 (0.853) | 0.074(0.312) | 0.054 (0.346) |
| March | -0.092 (0.713) | -0.109 (0.740) | 0.092(0.282) | 0.072 (0.303) |
| April | -0.038 (0.593) | -0.117 (0.772) | 0.110(0.235) | -0.003 (0.494) |
| May | -0.006 (0.524) | -0.248 (0.975) | 0.105(0.252) | 0.017 (0.443) |
| June | -0.083 (0.727) | -0.248 (0.985) | 0.070(0.318) | 0.183 (0.094) |
| July | -0.071 (0.722) | -0.178 (0.940) | 0.039(0.406) | 0.180 (0.093) |
| August | -0.229 (0.959) | -0.169 (0.859) | 0.015(0.457) | 0.036 (0.398) |
| September | 0.002 (0.483) | -0.097 (0.761) | 0.027(0.426) | -0.056 (0.638) |
| October | 0.018 (0.448) | -0.117 (0.799) | 0.048(0.379) | -0.037 (0.595) |
| November | 0.133 (0.187) | 0.010 (0.474) | 0.068(0.327) | 0.005 (0.483) |
| December | 0.001 (0.494) | -0.105 (0.763) | 0.071(0.334) | 0.004 (0.481) |

mechanisms that prevent the identification of a more significant co-occurrence pattern among frugivorous birds and fruit trees in urban environments.

The network analysis results show that some fruit tree species are critical to the frugivorous bird species-fruit tree species network. The top three fruit tree species are Amur honeysuckle, Chinese Juniper, and Oriental persimmon. A diverse range of frugivorous bird species consumed the fruits of these three species. Birds' preference for fruits is closely related to color, size, and quantity (Howe 1980; Sorensen 1981). Birds have keen color vision and prefer to feed on brightly colored fruits with no shells (Fischer and Chapman 1993; Link and Stevenson 2004; Lomáscolo et al. 2008). The fruit colors of these three species are red, brown, and orange, respectively, which align with these characteristics. Birds also prefer to feed on small fruits (Howe 1980). Amur honeysuckle and Chinese Juniper are small in diameter (5-6 and 4-9 mm, respectively), making them preferable to many species. Although Oriental persimmon has a large diameter (20-85 mm), its ripe fruits are soft and can be readily consumed by pecking. Moreover, plants that produce more fruit tend to attract birds more frequently (Schleuning et al. 2011). These three tree species produce abundant fruits. Field observations also provide evidence that birds in Beijing are attracted to these fruit tree species (He et al. 2021).

Our findings support two sets of recommendation for conserving frugivorous bird species in urban areas. First, planting fruit tree species can help preserve urban frugivorous birds. Our results showed a significant positive relationship between the species richness of frugivorous bird and fruit tree species at a monthly scale. The significant relationships during the winter and spring indicates the essential role of fruit trees as food resources for frugivorous birds. Second,

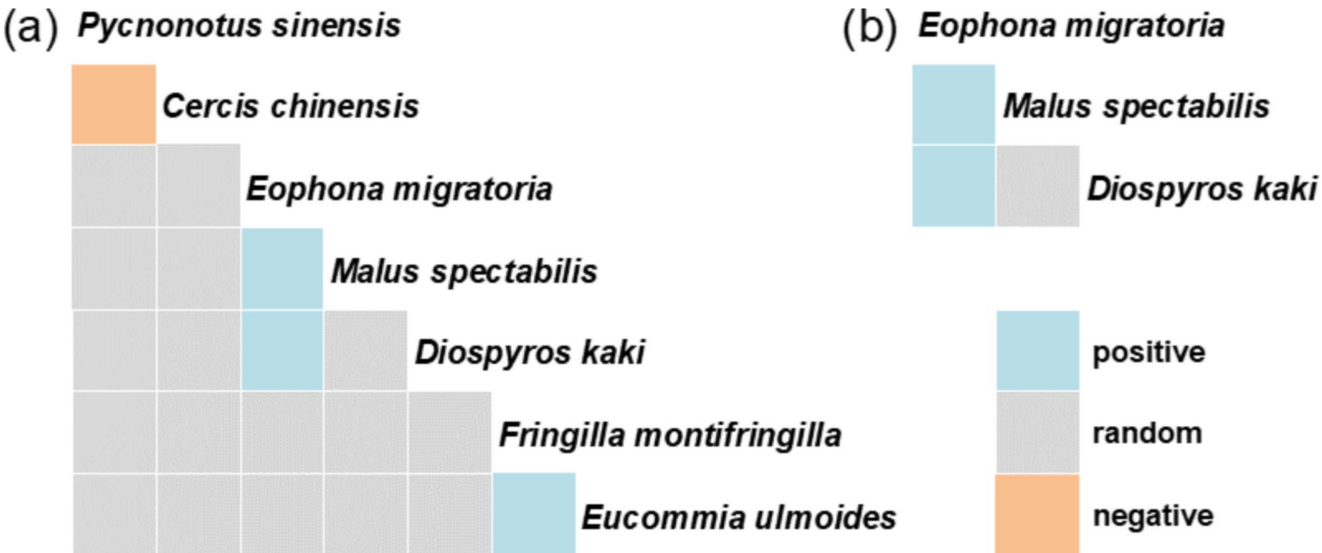


**Fig. 4** The significant co-occurrence of frugivorous bird and fruit tree species pairs based on their (**a**) potential and (**b**) realized interactions

**Fig. 5** The web of realized interactions between frugivorous bird and fruit tree species in 17 parks in Beijing China. The green rectangles represent the fruit tree species, and the orange rectangles represents the frugivorous bird species, with the species photos displayed alongside each rectangle. The width of each rectangle is proportional to the number of species it interacts with. The lines between the rectangles indicate feeding relationships between the frugivorous bird species and fruit tree species

due to the lack of significant associations between the species composition of the frugivorous bird and the fruit tree communities, a priority should be given to maximize fruit production of some "generalist" fruit tree species rather than match frugivorous bird species with fruit tree species. In Beijing, Amur honeysuckle, Chinese Juniper, and Oriental persimmon are suitable species to plant, as they support most frugivorous bird species.

While our study provides valuable information for understanding the inter-species interactions across trophic levels in urban environments, several limitations should be noted. We used citizen science (bird occurrence) data to explore the relationships between frugivorous bird and fruit tree species. Bird records contributed by citizen scientists were known to be biased toward species that are more detectable and charismatic (Isaac et al. 2014). Field survey data may

**Table 4** The results of three network indices from the network analysis of frugivorous bird and fruit tree species pairs in 17 parks in Beijing, China

| Tree species | Species degree | Resource range | Species specificity |
|---|---|---|---|
| *Lonicera maackii* | 19 | 0.22 | 0.11 |
| *Sabina chinensis* | 12 | 0.52 | 0.21 |
| *Diospyros kaki* | 11 | 0.57 | 0.23 |
| *Sophora japonica* | 10 | 0.61 | 0.25 |
| *Morus alba* | 8 | 0.70 | 0.29 |
| *Fraxinus pennsylvanica* | 6 | 0.78 | 0.36 |
| *Magnolia denudata* | 6 | 0.78 | 0.36 |
| *Ulmus pumila* | 6 | 0.78 | 0.36 |
| *Broussonetia papyrifera* | 5 | 0.83 | 0.41 |
| *Ligustrum lucidum* | 5 | 0.83 | 0.41 |
| *Malus baccata* | 5 | 0.83 | 0.41 |
| *Malus spectabilis* | 5 | 0.83 | 0.41 |
| *Pinus tabuliformis* | 4 | 0.87 | 0.47 |
| *Platycladus orientalis* | 4 | 0.87 | 0.47 |
| *Acer truncatum* | 3 | 0.91 | 0.55 |
| *Armeniaca vulgaris* | 3 | 0.91 | 0.55 |
| *Fraxinus chinensis* | 3 | 0.91 | 0.55 |
| *Malus × micromalus* | 3 | 0.91 | 0.55 |
| *Prunus salicina* | 3 | 0.91 | 0.55 |
| *Amygdalus triloba* | 2 | 0.96 | 0.69 |
| *Malus halliana* | 2 | 0.96 | 0.69 |
| *Robinia pseudoacacia* | 2 | 0.96 | 0.69 |
| *Crataegus pinnatifida* | 1 | 1.00 | 1.00 |
| *Photinia serratifolia* | 1 | 1.00 | 1.00 |
| *Pinus bungeana* | 1 | 1.00 | 1.00 |
| *Prunus tomentosa* | 1 | 1.00 | 1.00 |
| *Punica granatum* | 1 | 1.00 | 1.00 |
| *Sorbus pohuashanensis* | 1 | 1.00 | 1.00 |

be used to correct the sampling biases in birdwatching data. In addition, we did not use bird abundance estimates in the analysis due to the high uncertainty associated with the data. This limitation might be overcome in future studies through the use of alternative analytical methods (Johnston et al. 2021). Despite these limitations, our findings generated new insights into the relationships between frugivorous bird and fruit tree species in urban parks.

## Conclusion

Knowledge of the relationships between frugivorous bird and fruit tree species across trophic levels is crucial for understanding the mechanism shaping urban biodiversity. This study analyzed the association between urban frugivorous birds and fruit trees at both the species and community levels. Our results revealed a significant positive relationship between the species richness of frugivorous bird and fruit tree species at the monthly scale. The park area did not impact the relationship significantly, but the interaction effect of the park area and the richness of fruit trees was associated with the richness of frugivorous birds significantly in March, August, November, and December. However, this relationship was not evident based on community composition. Additionally, we identified the fruit tree species that are key to the network between frugivorous bird species and fruit tree species. Based on our results, we recommend planting fruit trees to preserve urban frugivorous birds and prioritizing maximizing tree fruit production when maintaining urban green spaces. Our study provides valuable information on the inter-species relationships across trophic levels in urban regions. Future studies can build upon our research to further explore the patterns and dynamics between frugivorous bird and fruit tree species in urban areas.

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**Author contributions** Jun Yang conceived the research idea. Jun Yang and Xingyi Liu developed the research design. Material preparation, data collection, and analysis were performed by Xinyi Liu, Xudong Yang, and Xingyu Li. The first draft of the manuscript was written by Xinyi Liu and Jun Yang and all authors commented on the draft. All authors read and approved the final manuscript.

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**Data availability** No datasets were generated or analysed during the current study.

## Declarations

**Competing interests** The authors declare no competing interests.

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