Landscape and Urban Planning 272 (2026) 105647

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Urban plant communities shape plant–bird frugivory interaction networks through reduced connectance and increased modularity

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HIGHLIGHTS

- Landscape plants structured frugivory networks with lower connectivity but higher modularity.
- Plant selection shaped birds' connector roles within urban plant–bird networks.
- Landscape and non-landscape plants generated distinct plant–bird interaction patterns.
- Diverse plant types in urban planning support network stability and bird conservation.

ARTICLE INFO

Keywords:
Plant–animal interactions
Plant–frugivore network
Urban biodiversity
Urban green space
Urban plants

ABSTRACT

Rapid urbanization is fundamentally reshaping plant–animal interactions that sustain urban ecosystem services and biodiversity. Plant–bird frugivory interactions represent critical mutualistic relationships that illustrate these impacts. Understanding how network structures vary between landscape and non-landscape plant species provides novel insights for designing resilient urban social–ecological systems. Here, we surveyed nine urban green spaces across Hangzhou, China, over nine months using arboreal infrared cameras to document frugivory interactions of birds with both landscape and non-landscape plants. We recorded 2,149 independent frugivory interactions, comprising 176 unique pairwise interactions between 30 plant species and 36 frugivorous bird species. Network analysis showed that frugivory networks involving landscape plants exhibited lower connectance and higher modularity compared with those involving non-landscape plants. Twenty bird species occurred in both network types, linking the entire urban plant–bird network. Furthermore, these shared species overall exhibited significantly higher betweenness centrality and among-module connectivity in the landscape network than in the non-landscape network, and some of them played markedly different roles between the two network types. Our findings reveal that landscape plants significantly alter network architecture and reconfigure bird functional roles, potentially impacting the stability of frugivorous bird-driven ecosystem services, given the prevalence of landscape plants in cities. More broadly, we highlight that plant selection within urban landscapes is not simply a design choice but a key determinant of ecological connectivity and resilience. Integrating diverse plant communities into urban planning frameworks can strengthen ecological network stability and ultimately support biodiversity conservation in rapidly urbanizing regions worldwide.

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https://doi.org/10.1016/j.landurbplan.2026.105647
Received 22 September 2025; Received in revised form 9 February 2026; Accepted 31 March 2026
Available online 3 April 2026
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1. Introduction

Urbanization has been expanding globally and has become one of the main drivers of global biodiversity loss (Newbold et al., 2015; Simkin et al., 2022). Understanding how species interactions are modified within urban environments has become critical for maintaining biodiversity and ecosystem services in urban areas (Aronson et al., 2017; Seto et al., 2012). Urban ecosystems often harbor novel communities dominated by urban-adapted and human-managed species, which can simplify community structure (Maxwell et al., 2016) and disrupt the complex species interactions essential for ecosystem stability (Mendes et al., 2025). Importantly, the loss of species interactions may occur even when species persist, producing an "empty forest syndrome" (Redford, 1992). In this syndrome, species interactions disappear prior to extinctions, particularly when keystone species or key processes, such as seed dispersal and pollination, are affected (Valiente-Banuet et al., 2015). This phenomenon indicates that urbanization inflicts more severe yet cryptic impacts on biological communities than previously recognized. Therefore, it is urgent to investigate how urbanization reshapes species interactions for the development of effective strategies to maintain biodiversity and ecosystem services in increasingly urbanized landscapes (Bascompte, 2009; Theodorou, 2022).

Among various types of species interactions affected by urbanization, plant–animal mutualisms are especially vulnerable because urbanization alters the spatial and temporal availability of the resources required by both partners (Moreno-García et al., 2025). Plant–bird frugivory interactions (hereafter, plant–bird interactions) represent a critical mutualistic relationship that exemplifies these urbanization impacts and remain important for urban biodiversity conservation (Mendes et al., 2025). As a conspicuous component of urban biodiversity, birds play a vital role in key ecological processes, such as seed dispersal mediated by their consumption of urban fruit as a primary food resource. Complex plant–bird interactions generate diverse ecological niches that allow birds with different foraging strategies to coexist, thereby enhancing overall bird species diversity (Dehling et al., 2022). Moreover, birds engaged in diverse interactions with fleshy-fruited plants enhance their resilience to environmental disturbances by switching to alternative food resources when high-quality fruit resources (e.g., those with high energy content) become limited (Tryjanowski et al., 2018), thereby stabilizing bird communities in urbanized areas. Notably, plant–bird interactions contribute to plant reproduction by seed dispersal, regenerating patches of native vegetation to support urban biodiversity (Corral et al., 2021; Mubamba et al., 2022).

Ecological network analysis provides a powerful framework for characterizing these complex plant–frugivore interactions (Bascompte and Jordano, 2013), with network structure metrics revealing how fruit resources influence urban bird biodiversity and community composition (Hernández-Dávila et al., 2022; Li et al., 2025). Network-level structure metrics (e.g., connectance, modularity, and nestedness) reveal overall topology and complexity of the interactions between birds and plants (Dehling, 2018). Node-level metrics, such as species' centrality and module connectivity, quantify the relative importance of individual species in maintaining network structure and stability (Morán-López et al., 2020). Understanding the structure and dynamics of these interaction networks can help uncover the underlying organization of urban biological systems and generate new insights for urban biodiversity conservation (Wang et al., 2023).

Urban environments present substantial challenges for maintaining stable plant–bird networks that differ fundamentally from natural systems. In natural habitats, diverse plants with fleshy fruits provide spatially and temporally heterogeneous fruit resources that maintain both bird species diversity and network stability (Costa et al., 2020; Li et al., 2022). However, the architecture of plant–bird networks in urban habitats is reshaped by complex anthropogenic drivers across multiple scales (Guerra et al., 2025). At the landscape level, land-use change and associated human-disturbance gradients can create sharp discontinuities in plant–bird interactions, thereby reshaping interaction patterns across space (Martins et al., 2022). Furthermore, intensive human management, such as human-selected plant transplants, frequent pruning, chemical application, and human activities, significantly alters fruit phenology and bird foraging behaviors, thus altering the structure of networks (Liu et al., 2025).

Under these landscape-level constraints and management pressures, the prevalence of human-selected landscape plants emerges as a bottom-up driver that determines the food resources base (Li et al., 2025), creating novel scenarios that largely modify plant–bird interactions. Landscape plants are often documented to exhibit markedly different characteristics, including limited diversity, spatially clustered distributions, and synchronized fruiting phenology (Wheeler et al., 2017). These altered resource characteristics are expected to favor opportunistic generalists that effectively exploit abundant but temporally concentrated resources (Callaghan et al., 2019), potentially reducing niche differentiation among birds and homogenizing plant–bird interaction networks (Schneiberg et al., 2020). Thus, urban vegetation shifts towards the landscape plants may facilitate the adaptation of dietary generalists to urban environments, but could also impede the persistence of dietary specialists via intensified competition (Gómez-Martínez et al., 2025). Networks dominated by generalists are hypothesized to be more modular but less nested, increasing their vulnerability to perturbations (Thébault and Fontaine, 2010). Moreover, such a shift could trigger cascading effects within the network, whereby changes in fruit availability reshape plant–bird interactions and propagate indirect consequences to other species (Rogers et al., 2021). These cascading effects, driven by the transition to landscape plants, may erode seed dispersal of non-landscape plants and weaken the stability of urban bird communities, particularly in more modular networks (Palacio et al., 2016; Thébault and Fontaine, 2010).

While such urban vegetation shifts represent a fundamental consequence of urbanization and largely alter species interaction networks, few studies have quantitatively compared the structures of plant–bird networks and functional roles of birds within networks involving landscape versus non-landscape plants in urban areas. Although landscape plants, particularly trees, increasingly balance both ornamental appeal and ecological functions (Ives et al., 2016), their selection, spatial configuration, and subsequent management often remain primarily driven by aesthetic and cultural purposes (Gobster et al., 2007; Xu et al., 2025). Importantly, these practices rarely aim to sustain trophic interactions or support the persistence of higher-trophic-level communities. This human-induced vegetation, distinct from the ecological processes governing non-landscape vegetation, potentially leads to interaction networks that are fundamentally distinct from those observed in natural habitats (Mendes et al., 2025). This knowledge gap constrains our ability to develop effective urban green space planning strategies for bird biodiversity conservation.

Here, we conducted a comparative analysis of plant–bird networks between landscape and non-landscape plants in urban green spaces of Hangzhou, Zhejiang Province, China. Using innovative arboreal camera traps that enable non-invasive, high-resolution documentation of plant–bird interactions on the trees (Zhu et al., 2022; Zhu et al., 2021), we compiled comprehensive datasets for interactions between birds and both landscape and non-landscape plant communities. Specifically, our objectives were: (1) characterize the interaction patterns between birds and two types of plants (landscape and non-landscape plants) respectively in urban areas; (2) identify key birds that contribute to the stability of landscape plant–bird interactions in urban areas, and (3) compare bird species roles between networks formed by landscape versus non-landscape plants. By filling this knowledge gap, our study provides critical insights for evidence-based management of urban green spaces to conserve bird diversity and ecosystem functions.

2. Materials and methods

2.1. Study area and sampling sites

This study was conducted in Hangzhou (118.20°–120.37° E, 29.11°–30.34° N), a city located in the coastal region of eastern China (Fig. 1). Hangzhou lies on the southern flank of the Yangtze River Delta, at the lower reaches of the Qiantang River, and the southern terminus of the Beijing-Hangzhou Grand Canal. The total forest cover in Hangzhou city spans approximately 1,151,615 ha, accounting for ~ 25% of the total urban landscape (Zhu et al., 2024b). The typical vegetation of urban green areas in Hangzhou consists of mixed secondary forests, dominated by species such as *Camphora officinarum, Celtis sinensis*, and *Triadica sebifera*. The climate in Hangzhou is a typical subtropical monsoon with marked seasonality. The annual precipitation is 1628.6 mm, and the average temperature throughout the year is 16.4 ℃ (Liao et al., 2022). We selected nine urban green spaces across Hangzhou to conduct our plant–bird interaction surveys (Fig. 1), considering the diversity of fleshy-fruit plants, consistent accessibility for repeated monitoring, and habitat diversity. These urban green spaces encompass a variety of habitat types, including artificial urban parks, remnant natural hills with near-natural conditions, and forest parks featuring built pathways (Table S1), and are distributed from the city center to the urban fringes.

2.2. Study plant species

We classified the monitored 30 plant species (comprising 93.3% native species, Table S2) into two categories by referencing regional records regarding their landscape usage (Editorial Board of Flora of Zhejiang (New Edition), 2021; Yu, 2023): (1) landscape plants, which are commonly used in urban landscape planning, particularly in green spaces and along streets; (2) non-landscape plants, which grow naturally in semi-natural or natural habitats and are not used for landscape ornamentation. For each plant species, we selected at least three individuals to monitor the frugivory events.

2.3. Monitoring of plant–bird interactions

Frugivory interactions between birds and study plants were monitored within the selected urban green spaces. The peak ripening period for fruits in the subtropical regions of eastern China occurs in autumn and winter, mainly from May to the following January (Li et al., 2025; Zhu et al., 2022). Thus, we employed arboreal infrared cameras (Zhu et al., 2022) to monitor plant–bird interactions from May 2024 to January 2025, covering the full mature fruiting periods of all monitoring plants (Table S2). Briefly, cameras were positioned on adjacent trees or sturdy branches of target trees and oriented toward the fruit-dense sections. Each camera faced north or south to avoid unnecessary triggers due to sunrise and sunset. All cameras were deployed at a strong trunk with heights below eight meters, depending on the fruit density and camera sensor range. Fruitless and dead branches, as well as leaves obstructing the camera view, were removed to minimize false triggers caused by wind-induced vegetation movement (Zhu et al., 2022). Cameras operated continuously 24 h per day and seven days per week. Each camera trigger captured three photos and a 10-second video. Data retrieval and battery replacement were conducted every 20 to 30 days, corresponding to the ripening period of fruits. More details on the setup of arboreal camera traps can be found in Zhu et al. (2022).

All image data from arboreal camera traps were independently examined by at least two researchers to ensure accuracy for frugivory interactions. Images captured by the cameras were screened for definitive evidence of frugivory interactions, including pecking, fruit handling, and swallowing behaviors. Only clear frugivory interactions between birds and the target plants were recorded as valid interaction events. To quantify the interaction frequency, we counted the number of independent interaction events between birds and the target plant. An independent interaction event was defined as any visit by a bird species with clear frugivory behaviors to a target plant individual within a five-minute interval (Zhu et al., 2022). For each plant–bird pairwise

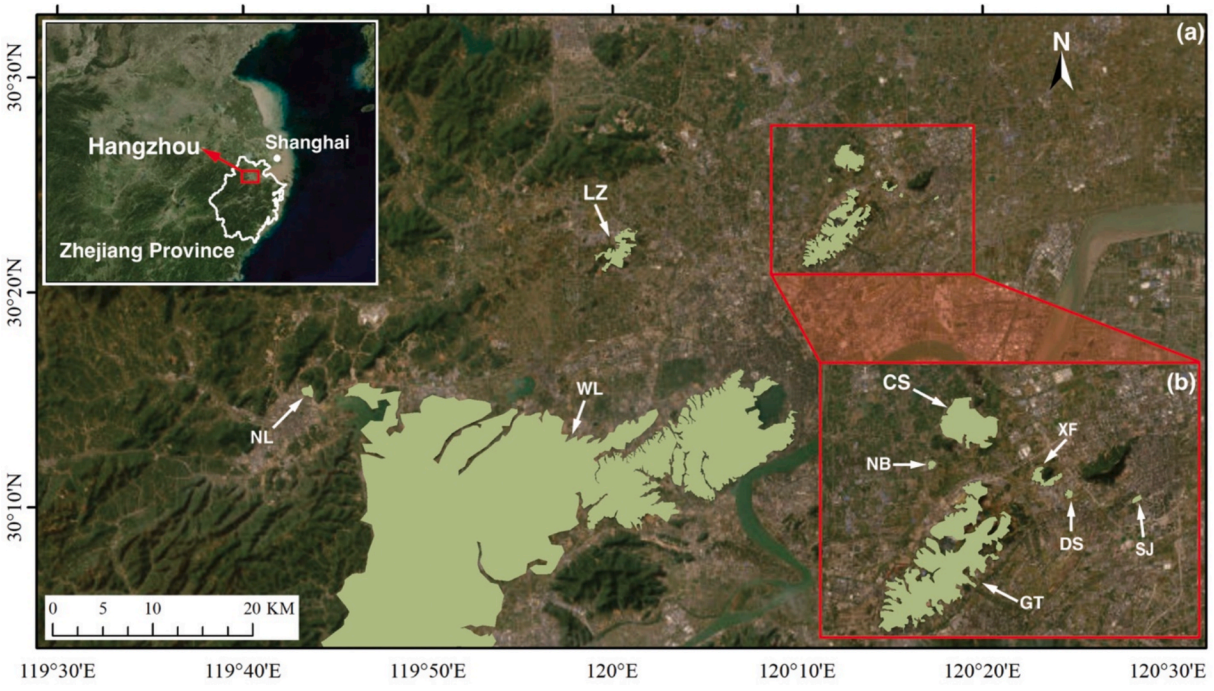

Fig. 1. Geographical location of the study sites in Hangzhou, Zhejiang Province, China. (a) Distribution of the nine studied urban green spaces (green polygons) overlaid on true-color satellite imagery. The inset map (top left) shows the geographical context of Hangzhou. (b) Magnified view of the area outlined by the red frame in panel (a), illustrating the spatial details and boundaries of the smaller study sites. Site codes (e.g., WL, GT) correspond to the site characteristics listed in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interaction, the final interaction frequency was calculated by summing all independent interaction events recorded across all monitored plant individuals. Finally, we obtained binary network matrices (based on the presence or absence of interactions) and quantitative network matrices (based on the frequency of interactions) to perform further network analyses.

2.4. Data analysis

2.4.1. Network structures of landscape versus non-landscape plant–bird interactions

We built plant–bird networks for both non-landscape and landscape plants (hereafter using non-landscape network and landscape network for simplicity). To test whether the structures of non-landscape and landscape networks differed from each other, we used weighted connectance, weighted nestedness (weighted NODF), and weighted modularity as metrics for quantitative network analyses, and used connectance, nestedness (NODF), and modularity as metrics for binary network analysis. We also built the networks across different seasons (summer, May to October, and winter, November to January in the next year) to further explore the variation of network structures.

Connectance refers to the density of interactions, calculated as the proportion of observed unique pairwise interactions to all possible interactions (i.e., the product of the number of plants and birds) in the network (Jordano, 1987). Nestedness describes a pattern in which specialist species interact with a subset of the partners of generalists; for example, plants visited by specialist birds are largely a subset of those visited by generalist birds (Bascompte et al., 2003), computed as the NODF metric based on the overlap of interactions and decreasing fill (Almeida-Neto et al., 2008). Modularity describes the pattern of species forming densely connected subsets (i.e., modules) (Olesen et al., 2007), which was computed using DIRTLPAwb + algorithm (Beckett, 2016). Network-level metrics were calculated using the *networklevel* and *computeModules* function in the R package *bipartite* v.2.18 (Carsten F. Dormann et al., 2022).

2.4.2. Bird species roles in landscape versus non-landscape networks

To compare whether bird species played different roles in the non-landscape versus landscape network, we calculated species-level metrics of network centrality and contribution to nestedness. We used closeness centrality to quantify the proximity of a focal species to all other species in the network, and betweenness centrality to assess the role of a focal species as a key connector between different parts of the network (Martín González et al., 2010; Zhu et al., 2024a). Species with greater contributions to nestedness are more likely to enhance the long-term persistence of interaction networks (Saavedra et al., 2011). Network centrality metrics were calculated using *specieslevel* function in the R package *bipartite*. The nestedness contributions of each bird species were calculated using the *nestedcontribution* function with 999 randomizations (Saavedra et al., 2011). Positive values indicate that a bird consumes a subset of the fruits foraged by generalists, which promotes the nested structure of the network. Conversely, negative values indicate that a bird consumes distinct or peripheral fruits ignored by generalists, thereby reducing the overall nestedness of the network.

To further describe the bird species roles in the networks, we constructed the combined urban plant–bird networks, including all birds and plants. We then further classified all species into four functional roles based on their modular connectivity in the combined network. Specifically, we used the within-module connectivity (Z value) to assess the relative connectivity of a focal species to other species within its own module, and the among-modules connectivity (C value) to evaluate the extent to which a species connects across different modules (Olesen et al., 2007). The Z and C values were calculated using *czvalues* function in R package *bipartite* v.2.18 (Carsten F. Dormann et al., 2022).

Thresholds for identifying species roles of birds were determined using the 95th percentile of the Z and C value distributions across all species in the networks, ranked from lowest to highest (Dáttilo et al., 2016; Zhu et al., 2025). Based on this framework, species were assigned to four roles (Olesen et al., 2007): (1) peripheral species (low Z and low C, both below the threshold), having only a few links and almost always only to species within their module; (2) module hubs (high Z and low C), highly connecting species linked to many species within their own module; (3) connectors (low Z and high C), linking several modules; and (4) network hubs (high Z and high C), acting as both connectors and module hubs.

2.4.3. Statistical analyses

To ensure a fair comparison of network structures between the non-landscape and landscape networks under different sampling efforts, we standardized interaction frequency by rarefying both networks to an equal number of interaction events. Specifically, we calculated network-level metrics for the observed non-landscape network, which involved fewer interaction events (N = 779) than the landscape network (N = 1370). For the landscape network, we built 1,000 null networks by randomly resampling the same number of interaction events as recorded in the non-landscape network. For each null network, we calculated network-level metrics and used these to estimate standardized effect sizes (z-scores) for the non-landscape network. Z-scores were calculated by subtracting the mean of the null metrics from the observed value and dividing by the standard deviation of the null distribution. This procedure allowed us to quantify how strongly the observed non-landscape network deviates from expected patterns derived from the landscape network under an equivalent sampling intensity. For modularity calculations, we ran the algorithm 100 times for each network to obtain the highest modularity value, as modularity optimization can yield different results due to its stochastic nature (Beckett, 2016). Species' modular connectivity (Z and C values) was then calculated based on module grouping under the highest modularity value. For both the observed non-landscape and the landscape network, we calculated species-level metrics for all bird species involved, respectively. To compare the roles of shared species between the two networks, we scaled all species-level metrics within each network using a z-score transformation. Given the non-normality of most metrics, we used the pairwise Wilcoxon signed-rank tests to compare bird species roles between the non-landscape and landscape network for shared bird species occurring in both networks. All statistical analyses were conducted in R software v4.2.1.

3. Results

We recorded a total of 2,149 independent plant–bird interaction events across all study sites, comprising 176 unique pairwise interactions between 30 plant species and 36 bird species. Among them, the landscape network accounted for 1,370 interaction events involving 19 landscape plant species and 34 bird species (Fig. 2a), while the non-landscape network contained 779 interaction events, with 11 non-landscape plant species and 22 bird species (Fig. 2b). Across the urban area, Light-vented Bulbul (*Pycnonotus sinensis*) was the most frequent bird that interacted with plants (N = 826), followed by Japanese White-eye (*Zosterops simplex*) (Table S3).

In summer, there were 1,020 independent plant–bird interaction events, comprising 387 interaction events between landscape plants and birds and 633 interaction events between non-landscape plants and birds. In winter, there were 1,129 independent interaction events, mainly comprised of landscape plant–bird interaction events (N = 983), while there were only 146 independent interaction events between non-landscape plants and birds.

3.1. Network topology comparison between the landscape and non-landscape plant–bird interactions

Overall, the landscape network showed lower connectance than the

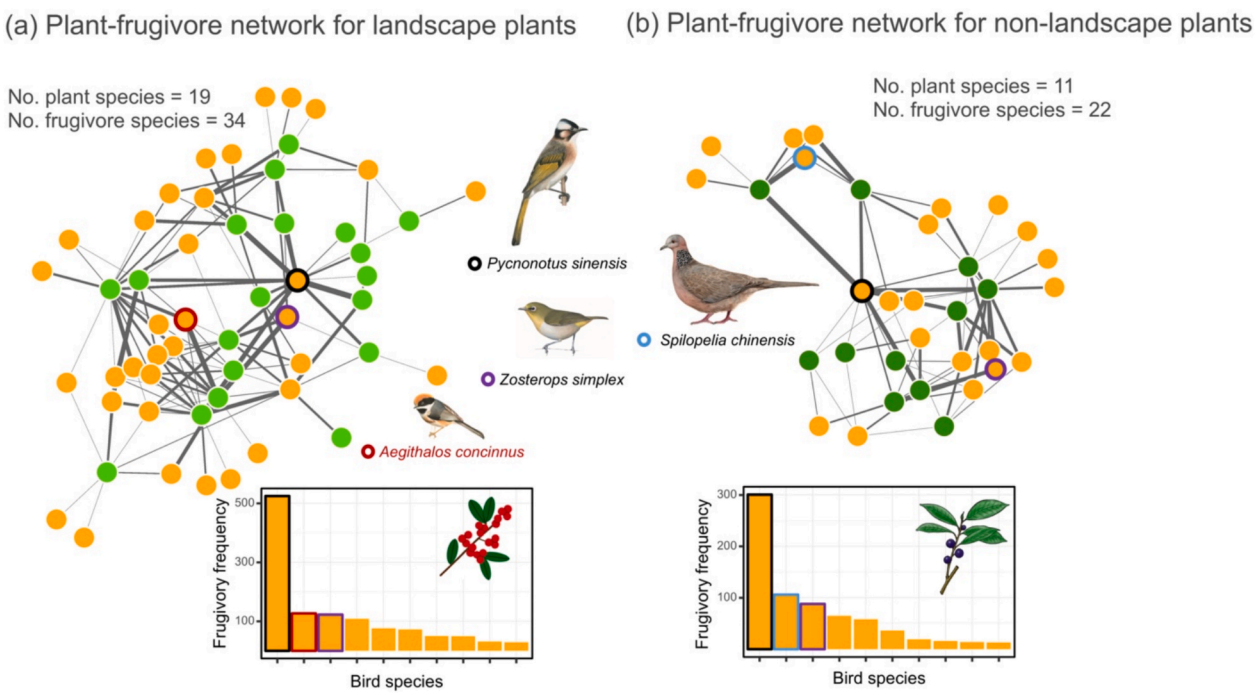

Fig. 2. Plant–bird interaction networks for landscape plants (a) and non-landscape plants (b). The visualization of the networks follows a force-directed graph drawing that organizes nodes (i.e., species) with higher centrality to more central positions. Line thickness is proportional to the logarithm of interaction frequency (i.e., independent interaction events) between species pairs. Green circles represent plant species (light green: landscape plants, $n = 19$; dark green: non-landscape plants, $n = 11$), and orange circles represent bird species. The three most abundant bird species in each network are outlined in color. The bar plots below show the frugivory frequency (i.e., number of interaction events) of the top ten bird species per network. Illustrations of representative landscape (*Pyracantha fortuneana*) and non-landscape (*Eurya muricata*) plants were drawn by Chen Zhu. Bird drawings were produced by Bai Xiao, Liang Su, Xiaodong Li, and Hao Ding. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

non-landscape network under the same total interaction frequency in both binary ($z = 9.77$, $p < 0.001$) and quantitative metrics ($z = 4.70$, $p < 0.001$; Fig. 3a, d). In contrast, nestedness showed no significant difference between the landscape and non-landscape networks (binary network: $z = 0.06$, $p = 0.95$; quantitative network: $z = 0.93$, $p = 0.35$; Fig. 3b, e). For modularity, the binary network showed no significant difference ($z = -0.12$, $p = 0.90$; Fig. 3c), but the quantitative landscape network was significantly more modular than the quantitative non-landscape network ($z = -5.11$, $p < 0.001$; Fig. 3f).

Seasonal analysis further confirmed that the landscape network consistently displayed lower connectance and similar nestedness compared to the non-landscape network. Specifically, connectance was lower in the landscape network during both summer (binary network: $z = -8.99$, $p < 0.001$; quantitative network: $z = -1.85$, $p = 0.06$, Fig. S1) and winter (binary network: $z = 5.46$, $p < 0.001$; quantitative network: $z = 2.88$, $p = 0.004$, Fig. S2). However, modularity exhibited seasonal variations: in summer, the landscape network was more modular in binary form ($z = 2.07$, $p = 0.04$) but less modular in quantitative form ($z = -8.80$, $p < 0.001$) (Fig. S1c, f). In winter, the landscape network was consistently more modular across both binary ($z = -3.03$, $p = 0.003$) and quantitative ($z = -2.56$, $p = 0.010$) forms (Fig. S2c, f).

3.2. Species roles of birds in urban plant–bird networks

There were 20 bird species shared between the landscape and non-landscape networks (Fig. 4). Based on the combined urban plant–bird networks, we identified two module hub species: the Chestnut bulbul (*Hemixos castanonotus*) and the Japanese white-eye. We also detected three connector species, including the Black bulbul (*Hypsipetes leucocephalus*), the Mountain bulbul (*Ixos mcclellandii*), and the Red-flanked bluetail (*Tarsiger cyanurus*). These five birds were shared species across both network types and possessed generalized diets (Table S3). Notably, two non-landscape plant-preferred birds (Mugimaki flycatcher *Ficedula mugimaki* and Blue-and-white flycatcher *Cyanoptila cyanomelana*) exhibited relatively higher among-module connectivity compared to the remaining 14 bird species that exclusively forage on landscape plants.

In total, shared bird species exhibited higher species-level metric values in the landscape network compared to the non-landscape network (Fig. 5). Among these, betweenness centrality and among-module connectivity of shared species in the landscape network were significantly higher than in the non-landscape network ($p < 0.05$; Fig. 5 a, e). For the 20 shared species, Light-vented Bulbul was the most important species maintaining the structure for both landscape and non-landscape networks (Fig. 5), which had the highest nestedness contributions (Fig. S4).

Notably, we also found shifts in the ecological role of the same bird species between the two types of networks. The Light-vented Bulbul mainly contributed to nestedness in the landscape network but showed reduced importance in the non-landscape network, while the Japanese White-eye contributed maximally to the nestedness pattern of the non-landscape network but negligibly to the landscape network. Interestingly, several common urban species, such as the Spotted Dove (*Spilopelia chinensis*), Japanese Tit (*Parus minor*), Chinese Blackbird (*Turdus mandarinus*), and Red-billed Starling (*Spodiopsar sericeus*), promoted the nested structure (positive contribution values) of the landscape network while reducing the overall nestedness (negative contribution values) of the non-landscape network (Fig. S1).

4. Discussion

In this study, we characterized the structural differences and species roles of birds within landscape and non-landscape plant–bird networks

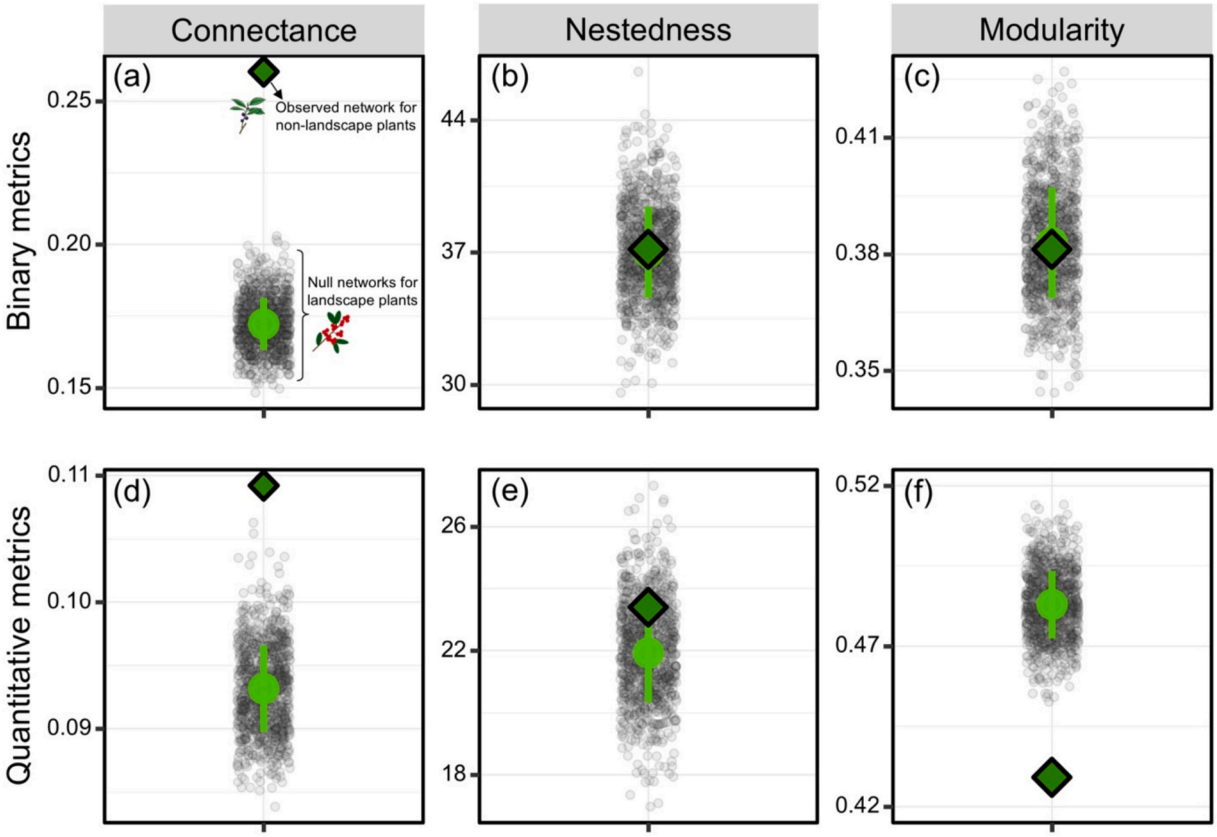

Fig. 3. Network-level structural parameters for the non-landscape and landscape networks in binary and quantitative metrics. Binary metrics (based on the presence or absence of interactions) are shown in the upper panels (a–c), and quantitative metrics (based on the frequency of interactions) are shown in the lower panels (d–f). For each structural parameter, the observed non-landscape plant–bird network was compared against 1,000 null (i.e., resampling) landscape plant–bird networks (gray points) constructed by randomly resampling interactions to match the sampling effort of the non-landscape network (see Materials and Methods). Light green circles represent the means of the null distributions, with error bars indicating standard deviations. Dark green diamonds represent the structural parameter of the observed non-landscape network. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in a subtropical urban ecosystem. Our results reveal that the landscape network is characterized by lower connectivity but significantly higher modularity compared to the non-landscape network. Seasonal analysis further confirmed that the landscape network had lower connectance and similar nestedness compared to the non-landscape network. At the species level, we also identified that shared generalist birds—particularly those acting as module hubs and connectors—play a more prominent role in the landscape network, as evidenced by their higher centrality and connectivity metrics. Furthermore, we observed distinct shifts in the ecological roles of key bird species (e.g., Light-vented Bulbul) between the two network types. Together, these findings highlight how landscape plants reshape urban plant–bird interactions, suggesting that maintaining a diversity of both landscape and non-landscape plants is crucial for sustaining urban biodiversity and ecosystem functions.

4.1. Differences in topological structure between the landscape and non-landscape networks

We found that networks between landscape plants and birds exhibited low connectance (Fig. 3a) and high modularity (Fig. 3f) compared to networks involving non-landscape plants. These observed structural differences primarily stem from distinct fruit resource organization and plant–animal interaction dynamics in urban green spaces. Landscape plant communities often exhibit spatially homogeneous and clustered distributions and synchronized fruiting phenology across urban green spaces (Niu et al., 2023; Yang et al., 2015), creating predictable resource pulses that contrast sharply with the heterogeneous distribution of non-landscape plants. This enhanced predictability of fruit resources, shaped by human aesthetic preferences and management practices, encourages birds to develop strong associations with high-reward landscape plant species while reducing exploitation of less profitable options (Rumeu et al., 2020). Supporting this interpretation, generalist species such as Light-vented Bulbul, Japanese Tit, and Japanese White-eye exhibited lower normalized degrees in the landscape network compared to the non-landscape network (Table S4) in our study, indicating concentrated foraging efforts rather than broad resource exploitation. This foraging strategy promotes the formation of plant–bird interaction subgroups. Within these subgroups across urban patches, species interact intensively at the local scale, forming modules within the regional networks and thereby reducing overall network connectance (Zhu et al., 2023).

Beyond resource predictability, the structural differences may also reflect the functional matching between human-selected fruit traits and bird preferences (Li et al., 2025; Valenta and Nevo, 2020). Landscape plants are often chosen for conspicuous visual displays with largely clustered, colorful fruits. These human-selected fruit characteristics may effectively attract a specific subset of the urban birds, thereby further reinforcing modular patterns in the landscape network (Li et al., 2025). The increased modularity of the landscape network may stem from the occasional attraction of some birds that prefer non-landscape plants (e.g., Chinese hwamei Garrulax canorus and Mountain bulbul, Table S4) to landscape plants, particularly during periods of scarcity of fruits from non-landscape plants. These non-landscape specialist birds had low degrees in the landscape network (Table S4), primarily interacting with landscape plants (e.g., *Ligustrum lucidum* and *Ilex rotunda* with more bird

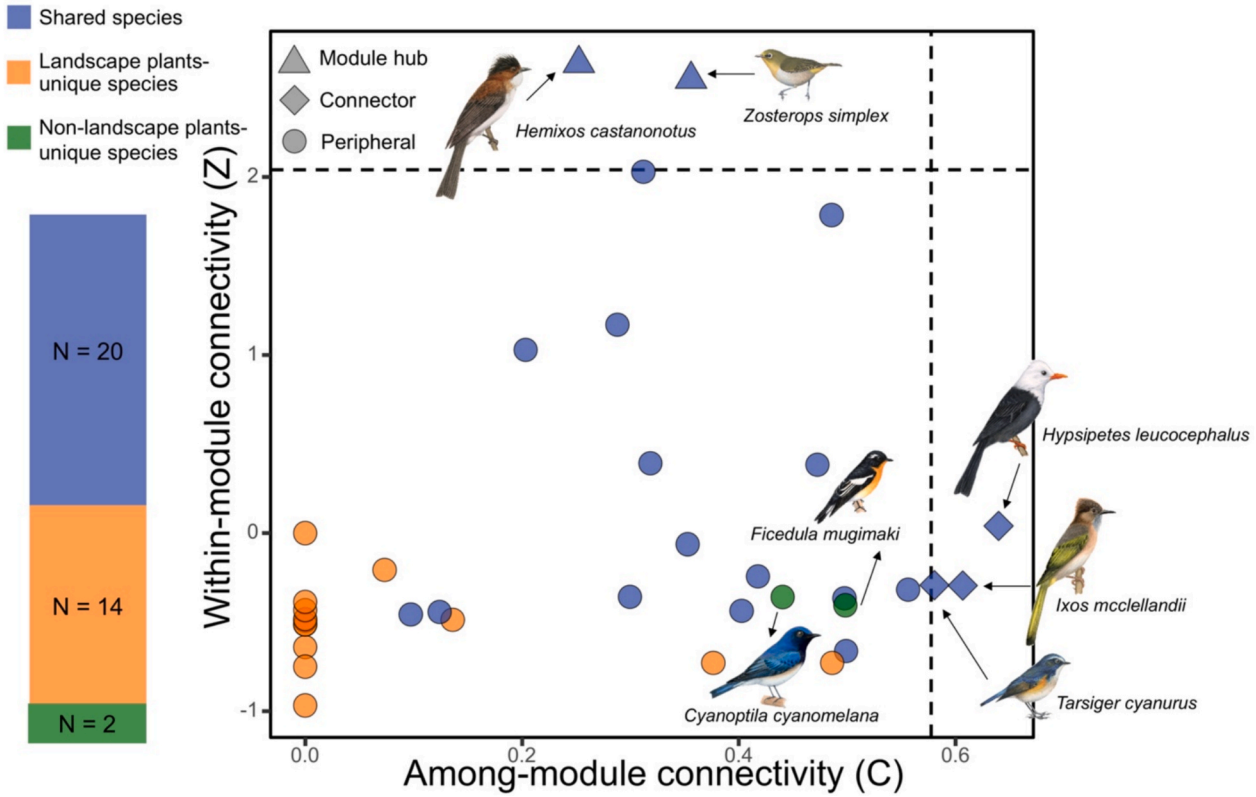

Fig. 4. Species roles in the modular structure of the combined urban plant–bird networks (including all birds and all plants). Species roles were classified based on the 95th percentile thresholds of within-module connectivity (*Z*) and among-module connectivity (*C*) (see Methods). Shared species are shown in blue, landscape plant-unique species in orange, and non-landscape plant-unique species in green. Modular core species (module hubs and connectors) and non-landscape plants-unique species were highlighted. Bird drawings were produced by Bai Xiao and Liang Su. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

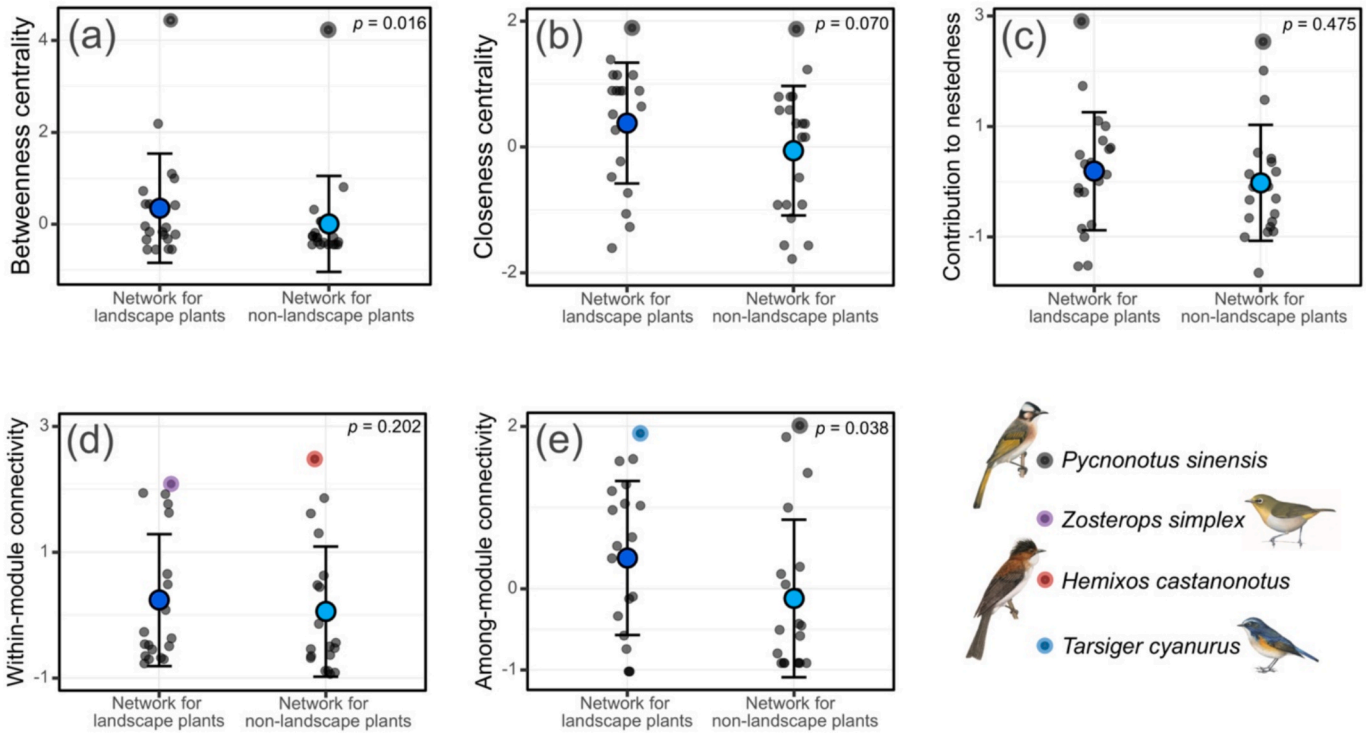

Fig. 5. Species-level metrics for shared bird species in the landscape and non-landscape plant–bird networks. Species-level metrics calculated from both networks were scaled (z-transformed) for the comparison of shared species. Wilcoxon signed rank tests were used to test for differences in species-level metrics between the two networks (see Methods). Species with the highest value in each metric were highlighted. Bird drawings were produced by Bai Xiao and Liang Su.

partners) that are central to the landscape network (Table S5). Attaching to the core modules in the landscape network, these opportunistic interactions create weak connections that further reduce overall network connectance while maintaining some degree of functional connectivity across plant types. Moreover, while urban environments typically offer abundant anthropogenic food subsidies, the availability of natural prey (e.g., arthropods) can be spatially or seasonally limited (Fenoglio et al., 2020). For bird species with high dietary plasticity—such as Pale thrush (*Turdus pallidus*) and Oriental magpie-robin (*Copsychus saularis*) observed in our study—landscape plants may offer a stable alternative resource, particularly during winter when natural prey becomes less accessible (Li et al., 2025; Zuckerberg et al., 2016). This behavioral shift potentially concentrates interactions within specific plant–bird modules, providing a plausible mechanism for the high modularity observed in the landscape network.

The association between lower connectance and higher modularity in ecological networks reflects the principle that sparse connections naturally cluster within functionally coherent groups rather than being randomly distributed across the networks (Zhu et al., 2023). Consequently, the high modularity in the landscape network likely results from the interplay between these intrinsic topological constraints and the ecological mechanisms driven by urban management practices, suggesting that human intervention can significantly influence the structural organization of mutualistic networks in urban environments.

Finally, our seasonal analysis revealed a temporal complementarity underlying these annual structures. While landscape plants dominated interactions during winter resource scarcity, non-landscape plants became the primary food sources in summer. The unexpectedly higher modularity of the quantitative non-landscape network in summer (Fig. S1f) may be driven by the invasive *Phytolacca americana*, which formed a distinct, highly connected module with generalist birds (e.g., Light-vented Bulbul and Spotted Dove) (Fig. S3), with interaction frequency disproportionately concentrated within this module. This finding suggests that while landscape planning dictates the baseline network architecture, some invasive species can temporarily distort interaction patterns during their fruiting peaks. Consequently, sustainable urban management requires not only maintaining landscape plants but also monitoring invasive species to prevent potential invasion risk facilitated by urban birds.

4.2. Bird species composition and functional roles across network types

4.2.1. Differences in bird species composition across two types of networks

We identified distinct patterns in bird composition associated with landscape and non-landscape plants (Fig. 4). Twenty bird species were shared between the two plant types, while landscape plants supported 14 unique bird species and non-landscape plants supported only two unique species (Fig. 4). This asymmetric pattern, with the landscape network exhibiting 7-fold higher unique species richness, suggests that landscape plants provide critical food resources for urban birds, particularly during resource-scarce winter periods when alternative food sources are limited (Li et al., 2025). The prevalence of shared species (20 out of 36 total bird species, 55.56%) across both networks indicates that these generalist birds have successfully adapted to exploit diverse food resources throughout urban landscapes, such as urban natural parks and human-managed urban green spaces. Moreover, these shared birds likely contribute to the persistence of sparsely distributed non-landscape plants in highly managed urban parks through their seed dispersal services, which may create important ecological linkages between patches in the urban matrix (Mendes et al., 2025; Zhu et al., 2025).

4.2.2. Keystone bird species in networks and their structural importance

Among these shared species, network analysis revealed that certain generalists play disproportionately important structural roles. In the combined network, we identified two hub bird species and three module connectors across all urban plants, all of which were shared generalist species (Fig. 4). These generalists possess broad dietary breadths and high behavioral plasticity, enabling them to exploit fluctuating resource availability characteristic of urban environments (Neate-Clegg et al., 2023). Their high dispersal capability further enhances their urban tolerance, which enables them to thrive in urban environments (Neate-Clegg et al., 2023). Thus, urbanization appears to act as a strong environmental filter that selects for generalist birds, with landscape plants serving as critical food resources supporting these urban-adapted bird communities (Li et al., 2025; Neate-Clegg et al., 2023).

Light-vented Bulbul emerged as the most structurally critical species for maintaining both landscape and non-landscape networks (Fig. 5). This finding aligns with well-documented ecological characteristics of this bird species as a highly adaptable, generalist bird with exceptional urban tolerance (Corlett, 2017; Lin and Liang, 2025). The important structural roles of Light-vented Bulbul across both network types can be attributed to several key functional traits: broad dietary spectrum encompassing both native and exotic fruits (Zhu et al., 2024a), and behavioral flexibility enabling exploitation of diverse foraging opportunities in human-modified environments (Chen and Wang, 2025). Notably, we also found that two bird species unique to non-landscape plant networks (Mugimaki flycatcher and Blue-and-white flycatcher) exhibited higher among-module connectivity values (Fig. 4). This pattern may result from two complementary mechanisms: (1) the non-landscape plants that birds rely on may act as resource “hotspots” (providing unique/scarce resources), thereby elevating the connectivity of their specialized bird visitors; (2) both Mugimaki flycatcher and Blue-and-white flycatcher are primarily insectivorous birds whose extensive spatial exploration behavior may increase their likelihood of interacting with different plants, thereby enhancing their connector roles within the network structure despite their preference for non-landscape plants. Thus, species’ functional roles in the network are largely shaped by their ecological characteristics and their ability to adapt to urban conditions.

4.2.3. Shifts in bird species roles between the landscape and non-landscape networks

The shared bird species consistently exhibited higher betweenness centrality and among-module connectivity in the landscape network compared to the non-landscape network (Fig. 5a, e), reflecting their enhanced role as “ecological bridges” in the more predictable landscape plant environment (Zhu et al., 2024a; Zhu et al., 2025). This is partly because landscape plants often possess conspicuous features, such as colorful fruits and open-area plantings (Wheeler et al., 2017), which readily attract a wide range of birds (Messeder et al., 2025) and promote their centrality within the network. Furthermore, this pattern likely stems from spatial concentration and phenological synchronization of landscape plants, which are often strategically selected and planted to create coordinated displays with synchronized flowering and fruiting periods (Lim and Sodhi, 2004). Such temporal synchronization creates resource pulses that attract diverse frugivore assemblages to specific locations and promote rapid dietary switching among co-occurring bird species (Carnicer et al., 2009). These factors force generalist birds to interact with broader arrays of plant species within concentrated timeframes and spaces, thereby increasing their network centrality as they bridge different plant–bird interaction modules. Conversely, the temporally dispersed and spatially scattered fruiting patterns of non-landscape plants may facilitate more specialized foraging strategies, resulting in lower overall network connectivity among shared species (Ramos-Robles et al., 2016).

We also documented dramatic shifts in individual species' nestedness contributions between the landscape and non-landscape networks (Fig. S4). For example, White's thrush (*Zoothera aurea*) exclusively promoted the nested structure of the non-landscape network. Some common urban-adapted bird species (e.g., Light-vented Bulbul, Chinese Blackbird, and Japanese Tit) promoted the overall nestedness of the landscape network but reduced the overall nestedness of the non-

landscape network (Fig. S1). This role plasticity suggests that landscape plant characteristics optimize the ecological function of urban generalists, while the spatially scattered and temporally dispersed nature of non-landscape plants may constrain these species' network centrality and primarily support those less urban-tolerant bird species.

4.3. Functions of landscape and non-landscape plants in frugivory and seed dispersal

The ecological consequences of seed dispersal services differ fundamentally between landscape and non-landscape plants based on their functional roles. Primarily, fleshy-fruited landscape plants act as a stable food resource (Li et al., 2025) rather than a source for natural recruitment, whereas non-landscape plants are key drivers of the regeneration of secondary forests in urban abandoned patches (Chen et al., 2025). The high connectance of non-landscape networks (Fig. 3) ensures seed dispersal in the semi-natural remnants by involving a diverse assemblage of frugivores, including urban-sensitive species. However, the lower connectance and higher modularity of the landscape network (Fig. 3) suggest spatially clustered fruit availability within particular habitats or seasons, which may attract birds foraging efforts away from non-landscape plants, thereby weakening the seed dispersal of non-landscape plants. Notably, dietary and habitat generalist bird species that forage flexibly on both landscape and non-landscape plants may function as critical “mobile links”, facilitating directed, long-distance seed transport across the fragmented urban matrix (Carlo and Morales, 2016; Zhu et al., 2024a). Consequently, the spatial configuration and fruiting phenology of landscape plants may shape seed dispersal patterns in urban areas and ultimately influence the regeneration of native vegetation in naturally regenerated patches (Corral et al., 2021).

4.4. Implications

First, urban landscape planning should transition from generic aesthetic planting toward a spatially stratified strategy that incorporates species roles in ecological networks into the conservation of urban biodiversity and ecosystem services (Harvey et al., 2017). We recommend diversifying landscape plant selection to provide temporally staggered fruiting periods and varied fruit morphologies, while strategically integrating semi-natural vegetation patches that support non-landscape plant communities and their associated specialist species. Specifically, in highly urbanized matrices (e.g., residential zones and streetscapes), planning could prioritize core landscape plants with high interaction strength and betweenness, such as *Triadica sebifera, Photinia serratifolia,* and *Broussonetia papyrifera* (Table S5). These plants can maintain core birds (e.g., Japanese White-eye, Red-flanked bluetail, and Black bulbul) and reinforce the topologies of the network. Conversely, in natural urban parks or green belts, retaining non-landscape plants (e.g., *Eurya muricata* and *Symplocos tanakana*) is important to provide refuges for habitat specialists, like Mugimaki flycatcher and Blue-and-white flycatcher. This combination of managed ornamental areas with less-intensive management zones can restrain the formation of highly connected modules, thereby promoting overall community stability in urban mutualistic networks (Thébault and Fontaine, 2010). Such integrated planning moves beyond traditional native-versus-exotic distinctions toward a more nuanced understanding of how different vegetation types contribute to urban ecosystem functionality, ultimately creating resilient green infrastructure that serves both human needs and biodiversity conservation objectives (Mubamba et al., 2022).

Second, monitoring ecological networks in urban environments can inform targeted conservation actions (Peng et al., 2024). For generalist birds that consume both landscape and non-landscape plants, such as the Chestnut bulbul (the module hub species) and Mountain bulbul (connector species) identified in our study, we recommend protecting their habitats in nearby naturally regenerating urban forests to facilitate movement among urban patches and enhance seed dispersal for non-landscape plants (Carlo and Morales, 2016). On the other hand, for specialist and urban-sensitive species that preferentially rely on non-landscape plants (e.g., Mugimaki flycatcher and Blue-and-white flycatcher), we suggest safeguarding natural-regenerating patches within urban areas and allowing natural regeneration with minimal human planting. Such patches can help maintain vegetation structural complexity and support bird diversity in urban environments (Dansereau et al., 2025). Taken together, our results fundamentally challenge traditional conservation paradigms that dismiss human-modified landscapes or solely plant the non-landscape plants, revealing the important role of different plant types in maintaining plant–animal communities and their interactions across fragmented urban environments.

4.5. Limitations and future direction

Several limitations should be acknowledged when interpreting the findings of our study. Our study focused on 30 fruit-bearing plant species (19 landscape and 11 non-landscape species) in Hangzhou. These species were selected based on their high ecological prevalence and functional role as major food resources for birds in the urban matrix. Although we utilized robust statistical approaches to address unequal sample sizes, it still represents a limited sample size of landscape plant pools. Additionally, although our selection of landscape plants covered a substantial proportion of plant–bird interactions in the urban area, it may not fully capture the contributions of rarer or seasonally ephemeral species that also exist in the urban plant pool. Future studies should aim to include more rare plant species by monitoring across broader spatial–temporal scales, thereby providing an even more comprehensive understanding of how urban management influences mutualistic network stability.

5. Conclusions

Understanding the structure of plant–bird networks can reveal the underlying organization of urban biological systems and provide critical insights for urban bird biodiversity conservation. Our findings demonstrate that landscape plant–bird networks exhibit distinct structural properties with lower connectance and higher modularity compared with the non-landscape network. Moreover, shared bird species displayed significantly higher betweenness centrality and among-module connectivity in the landscape network. This study expands research on urban biodiversity patterns by analyzing interaction-based biodiversity dynamics, highlighting the impact of plant types on plant–bird interactions and network structures in cities. Therefore, urban landscape planning should incorporate not only species- and community-level biodiversity patterns but also interaction networks to build biodiversity-friendly cities. To enhance the effectiveness of conservation for specific frugivore groups, future urban planning and management strategies should prioritize plant communities that contribute to stabilizing interaction networks and supporting sensitive species.

CRediT authorship contribution statement

Di Zeng: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Pengfei Xiang:** Writing – review & editing, Writing – original draft, Validation, Software, Investigation, Data curation. **Guoqingzi Chen:** Writing – review & editing, Validation, Investigation, Data curation. **Gengxian Hao:** Writing – review & editing, Validation, Investigation, Data curation. **Jing Guo:** Writing – review & editing, Validation. **Ping Ding:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Chen Zhu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation,

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Dr. Mingjian Yu, Dr. Chuping Wu, Dr. Xiaofeng Jin, Pengwei Chen, Minghao Sun, Xinjie Chen, and Yongjie Zhan for their assistance with project management, fieldwork, plant identification, and manuscript preparation. This study was supported by the National Key R&D Program of China (Grant No. 2023YFF1304600), "Pioneer" and "Leading Goose" R&D Program of Zhejiang (Grant No. 2024C03227), and Zhejiang A&F University Research Development Fund Talent Launch Project (Grant No. 2025LFR035).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2026.105647.

Data availability

The data are permanently archived in Figshare (https://doi.org/10.6084/m9.figshare.30022132).

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