

Bird-Tree Associations and Co-occurrence Patterns in Delhi: Implications for Urban Ecological Restoration and Invasive Species Management

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Abstract

Urban trees and birds are intertwined indicators of ecological resilience in cities. This study maps citywide bird-tree interactions in Delhi, India, hosting more than 300 avian species. The city was divided into hexagonal grids, and bird-tree data (506 interactions) were collected through field surveys across 131 sites using standardised 1-kilometre transects. Native keystone species like ficus supported the greatest bird diversity, while invasive *Prosopis juliflora* was widely used for perching and vocalisation. Native trees contributed significantly to bird richness and behavioural diversity, highlighting their restoration priority. This study is among the first to map bird-tree interaction network and assess its relationship in a megacity, combining bird-bird (mean $r=0.37$), plant-plant (mean $r=0.5$) and bird-plant (mean $r=0.07$) with only 5 pairs exceeding ($r=0.5$) co-occurrence analyses with behaviour-specific observations. This study offers pertinent facts to inform biodiversity-conscious urban restoration policies in swiftly growing cities. By embedding these patterns within an active *Prosopis juliflora* canopy-lifting programme, it provides rare, management-ready evidence on how native keystone trees and invasive cover jointly structure urban bird communities.

Keywords: Bird-Tree Interactions, Invasive Species, Urban Ecology, Habitat Complexity, Delhi City

1. Introduction

Bird-tree associations and co-occurrence patterns in Delhi are critical for understanding urban ecological restoration and invasive species management, particularly given the rapid urbanisation and its impacts on biodiversity (Chauhan et al., 2022; Rawal et al., 2023). Research in Delhi highlights how urban green spaces, including street trees and forest fragments, support avian biodiversity, but also face challenges from non-native and invasive plant species (Barhadiya et al., 2022; Chauhan et al., 2022; Rawal et al., 2023). Studies have shown that native tree species significantly influence bird communities in urban environments. For instance, *Ficus* (fig) trees, which are keystone resource providers in tropical landscapes, are a relatively common choice for street trees in Delhi and are associated with bird visitation (Rawal et al., 2022, 2023). The structure of urban green spaces, such as park size and tree canopy cover, also plays a crucial role in shaping bird diversity. Larger parks and those with higher mean tree cover generally support greater bird diversity and richness (Kumari et al., 2024; La Sorte et al., 2020). Moreover, a tree canopy cover exceeding 30% and the presence of native trees are known to enhance bird insectivory and tree biosecurity, supporting ecosystem services like pest control (Basile et al., 2025a, 2025b). However, the presence of invasive tree species poses a significant challenge to avian biodiversity and ecological restoration efforts in Delhi. *Prosopis juliflora* is a prominent invasive species in the semi-arid regions of India, including Delhi, which has been observed to alter native biodiversity and ecosystem functions (Gupta et al., 2024; R. et al., 2024). Studies from other regions also emphasise the widespread negative impacts of *Prosopis juliflora* on ecosystems and livelihoods (Eschen et al., 2024; Kamiri et al., 2024; Kishoin et al., 2024; Shiferaw et al., 2023).

The impact of non-native vegetation on bird communities varies. Some non-native species can provide resources to native fauna, especially in urban areas where native resources are scarce due to biotic homogenization (Deshpande et al., 2023). However, in Delhi, non-native plant forests generally support fewer bird species compared to native forests (Barhadiya et al., 2022). The removal of invasive trees has been shown to lead to bird community recovery (O'Leary et al., 2021). For instance, a study examining the removal of *Pittosporum undulatum* in Australia found that bird community composition shifted partially toward reference conditions following removal, although recovery was incomplete and varied among sites (O'Leary et al., 2021). Similarly, controlling invasive species is key to reducing threats to ecosystem viability and can improve the structure of ecological interaction networks (Marciniak et al., 2024). Ecological restoration strategies in urban environments need to consider these complex interactions. Prioritising native tree planting in urban greening initiatives can enhance ecological restoration outcomes by supporting trophic complexity and native bird conservation (Klaus & Kiehl, 2021). This aligns with the concept of urban ecology, which aims to design green infrastructure and manage wildlife to address biodiversity issues in cities (Chauhan et al., 2022; Klaus & Kiehl, 2021). Restoration efforts should focus on recovering historical reference states or at least improving site function, especially in irreversibly altered landscapes (Klaus & Kiehl, 2021). The inclusion of diverse native plant species is crucial for maintaining and enhancing urban bird diversity and ecological health (Elliot Noe et al., 2022; Schillé et al., 2025).

Furthermore, understanding bird-tree co-occurrence patterns can inform more effective urban forestry practices. Frugivorous birds and fruit trees exhibit strong associations, and analysing these interaction networks in urban parks can reveal structural differences and the role of generalist species (Liu, Yang, Li, et al., 2025; Liu, Yang, Zhou, et al., 2025). Citizen science data can be valuable in exploring these relationships, helping to identify how species richness and composition of frugivorous birds are linked to fruit tree species in urban settings (Liu, Yang, Li, et al., 2025). The selection of appropriate tree species for urban planting programs is vital. While exotic species might offer ornamental value, their ecological functions and potential invasiveness must be carefully evaluated (Deshpande et al., 2023). High tree species richness and diversity in urban areas, while often associated with increased overall biodiversity, can also increase the availability of suitable hosts for invasive tree pests and pathogens (Augustinus et al., 2024). Therefore, the choice between native and non-native species needs to be balanced, considering both the benefits to native fauna and the risks of introducing or exacerbating invasive species problems (Augustinus et al., 2024; Chauhan et al., 2022; Deshpande et al., 2023).

Researches shows that native plants, especially trees with complex structures, are very important for supporting a wide range of bird groups around the world (García, 2016). Mutualistic networks spanning continents illustrate that keystone tree species directly affect bird diversity and environmental resilience (Poisot et al., 2021). India is facing more and more problems on a national level because of urbanisation and the proliferation of invasive species. These species are damaging for native bird populations and the quality of their natural habitats. In Delhi, the urban landscape has a unique mix of native and exotic trees that have a direct effect on the birds that live there. There are also efforts to bring back native species and lessen the pressure from invasive species (O'Leary et al., 2021). Our study expands on this nuanced comprehension, concentrating specifically on avian-vegetation interactions within Delhi's urban framework.

Urban ecosystems are important for biodiversity protection, with the interaction between trees and birds acting as a key indicator of ecological health and resilience. Studies show that diverse tree species or polyculture farming practices enhance avian and other biodiversity by offering substantial resources (e.g., food, prey availability, and shelter), thereby improving foraging and nesting opportunities as compared to monoculture plantations (Yahya et al., 2022). This also applies to urban forest management, as different tree assemblages establish multidimensional habitat niches crucial for sustaining rich bird populations. The structural variety offered by diverse tree species is crucial in urban settings. Polyculture and agroforestry enhance habitat complexity, variety (e.g., tree species diversity), and microclimate regulation, hence improving habitat stand structure due to the stratification of plant layers (Yahya et al., 2022). This stratification is particularly vital in highly populated metropolitan regions where fragmented green spaces support biodiversity within constrained geographical limits. Individual trees have been extensively researched and are characterised as 'keystone structures' due to their disproportionate impact on the ecosystem relative to the area they occupy (Pustkowiak et al., 2021). The systematic plantation of trees in urban areas can significantly enhance conservation efforts, especially in fragmented areas.

In 2022, the Delhi government initiated a comprehensive initiative to mitigate the proliferation of the invasive *Prosopis juliflora* (Vilayati Kikar), a prevalent tree on the Delhi Ridge, through "canopy lifting" (pruning the upper canopy) and the introduction of indigenous tree species in its understory ("Six-Member Panel to Monitor Ridge's Restoration, Says Rai," 2021). This continuous initiative aims to diminish the dominance of *P. juliflora* without complete eradication, signifying an unparalleled urban habitat management endeavour. In this context, comprehending how Delhi's avifauna employs urban trees, both indigenous and non-native, is particularly relevant. Insight into the use of Vilayati Kikar and other trees as perches, foraging, and calling sites can inform whether such large-scale pruning and replanting efforts will sustain, or disrupt, the city's avifauna.

In Delhi, these ecological questions are inseparable from urban planning and policy. The Ridge and the emerging network of biodiversity parks are being actively redesigned through canopy lifting of *Prosopis juliflora* and under-planting of indigenous trees, while street-tree and park planting schemes are expected to deliver both climate-resilience and biodiversity benefits. Yet planners currently lack city-wide, species-level evidence on which tree assemblages maintain avian diversity, and how invasive structural cover can be removed without creating ecological bottlenecks. By quantifying bird-tree interaction patterns across Delhi and contrasting the roles of native keystone trees and invasive *Prosopis*, this study provides decision-relevant information for the design of Ridge restoration, biodiversity-park plantings and climate-resilient urban greening strategies.

The objectives of this study are to quantify bird-tree interaction patterns across Delhi's urban landscape, including behaviour-specific use (perching, calling, feeding, nesting and fiddling) of each tree species; to identify native and non-native tree species that act as keystone structures for urban birds by comparing the richness and composition of bird assemblages associated with each taxon; and to analyse bird-bird, plant-plant and bird-plant co-occurrence patterns using grid-based Pearson correlation matrices to detect species groups and habitat associations across the city. This study is distinctive in combining fine-scale, citywide bird-tree interaction data with parallel bird-bird, plant-plant, and bird-plant co-occurrence analyses in a highly urbanized megacity. By situating these analyses within Delhi's ongoing canopy-lifting and *Prosopis juliflora* under-planting programme, it offers timely, evidence-based insights for invasive-tree management and native-species restoration in dense urban landscapes.

2. Data and Methods

2.1. Study Area

The study was carried out in Delhi, with an area of 1400 km². The city is a part of the central Indo-Gangetic plain, sitting at the junction of strikingly different landscapes. To the west and south, the ancient Delhi Ridge, low hills of hard quartzite, supports dry deciduous woodland dominated by acacias, thorny shrubs and pockets of diverse tree species, offering the city its last vestige of semi-natural forest. Eastward, the land flattens into the Yamuna floodplain, where seasonal inundation creates belts of reed marsh, riparian woodland and a string of recent biodiversity parks that mimic lost wetlands. Scattered among these anchors are

irrigated fields on the northern and south-western fringes, plantations of Neem, Sheesham and Eucalyptus along canals and highways, and long, tree-lined avenues that introduce ornamentals such as Gulmohar, Amaltas and royal palm deep into the urban fabric. Accelerated urban expansion has overlaid Delhi with tightly knit residential enclaves, bustling commercial districts, and an intricate transport network, compressing the landscape into a steep gradient that runs from concrete-dominated city cores to scattered pockets of residual vegetation and peripheral farmland. The city's semi-arid, markedly seasonal climate sharpens this contrast: summer temperatures routinely surpass 45 °C, winter nights dip below 5 °C, and almost the entire annual rainfall arrives during the brief July-September monsoon. When these climatic swings intersect with persistent air and noise pollution, they create pronounced environmental shifts across surprisingly short distances, making Delhi an interesting setting for studying how biodiversity persists under the pressures of a rapidly growing megacity.

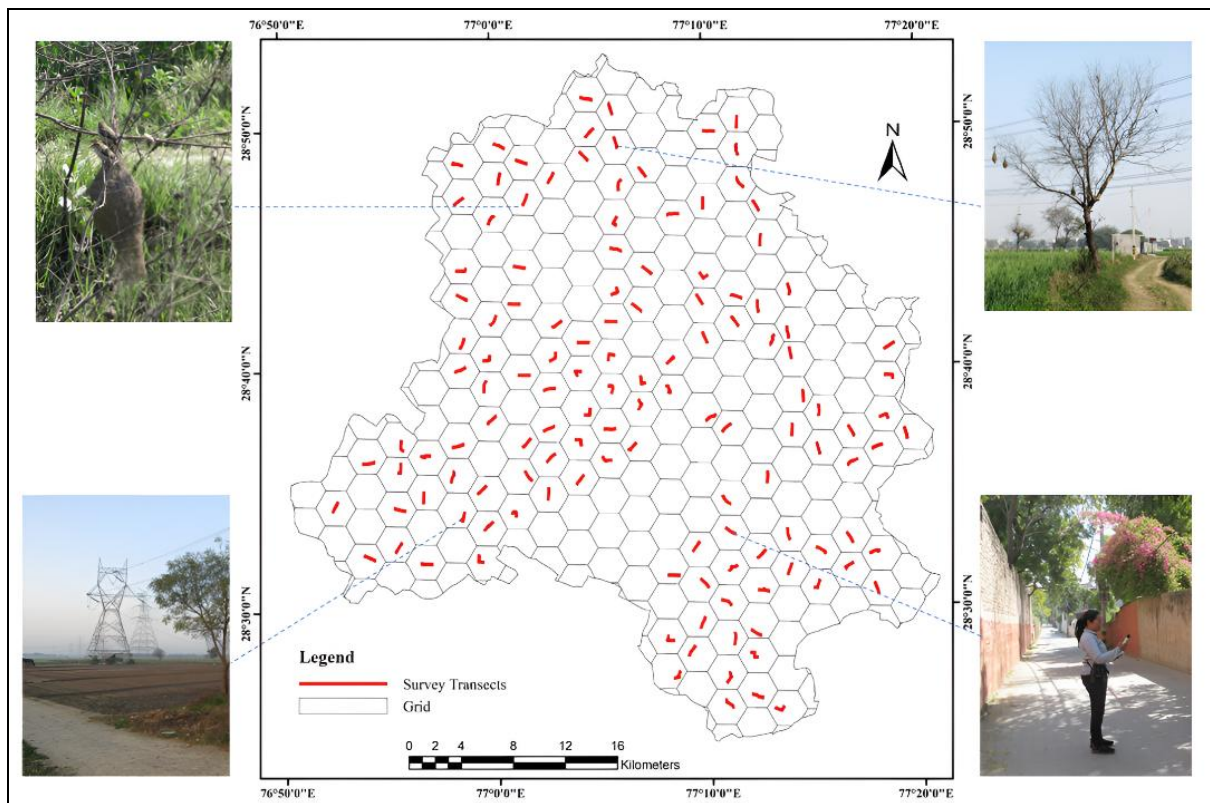


Figure 1: Map of the study area; red lines show the transects walked by the observer to collect the data.

2.2. Sampling and Survey

The polylines of transects measuring one km in length were delineated on the Google Earth Android application. Hexagonal grids with an area of 6.25 km² were generated in ArcMap v.10.8 via the Create Tesselation tool. Transects were selected based on logistical feasibility and accessibility, given time and resource constraints. Data collection was conducted on foot by walking the transects within defined grids. The sampling effort involved one individual. The data was collected from early December to mid-March. The designated period for data collection was from sunrise till 11 a.m. Binoculars were used to closely identify bird and

plant species, followed by photographic identification of plants using field guides. Each observation encompassed the avian species, the count of individuals, plant species, and the behaviours displayed by the birds over the 131 sampled grids. The data was compiled in Microsoft Excel 2019. The analysis was then carried out using Python from the Anaconda package. The initial step was to clean the information, remove extra spaces from heads and treat missing information to prepare the set ready for study.

The cleaned data were then transformed into numeric matrices, which represented how often each bird came to each plant, and how often birds and plants occurred at each of multiple locations on grids. These matrices were then used to construct all later analyses of correlation. In an effort to exclude deceptive results due to unusual observations, two filters were applied. The first used only those species which appeared at least three times over all of the data, and the second used an even more stringent threshold of five or more observations. Including these two thresholds, three different levels of analysis were carried out.

2.3. Correlation Metrics

Pearson correlation was used on three separate patterns: between bird species, between plant species, and between bird and plant species. For bird-bird correlations, birds were paired together based on which plants they visited. For plant-plant correlations, plants were paired together based on which birds visited them. Separate bird-plant correlations were then calculated for each grid such that comparisons were spatially consistent. Heatmaps were also generated to graphically illustrate the strength of association. Pearson correlation coefficients were calculated using the standard formula, where x_i and y_i represent the abundances of paired species (birds, plants, or bird-plant) in grid i , and $\bar{x}$ and $\bar{y}$ are their respective means across all 131 grids.

$$r = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^n (x_i - \bar{x})^2} \sqrt{\sum_{i=1}^n (y_i - \bar{y})^2}}$$

Where,

- $(x_i - \bar{x})$: How far each x_i is from the average of x (its deviation from the mean).
- $(y_i - \bar{y})$: How far each y_i is from the average of y .
- $(x_i - \bar{x})(y_i - \bar{y})$: Product of deviations; positive if both are above or both below their means, negative if one is above and the other below.
- $\sum (x_i - \bar{x})(y_i - \bar{y})$: Adds up all those products; this is the covariance (up to dividing by $n - 1$).
- The denominator $\sqrt{\sum (x_i - \bar{x})^2} \sqrt{\sum (y_i - \bar{y})^2}$ rescales by the spread (standard deviations) of x and y , so r always lies between -1 and 1 .

3. Results

3.1. Descriptive Statistics of Birds Behavior

The dataset contains 506 bird-plant observations spread across six behavioural classes. We distinguished five behaviour categories: perching, calling, feeding, nesting and “fiddling”, defined here as within-canopy movement - a bird moving among branches, leaves or twigs inside the tree crown without perching, feeding, calling or nesting. Perching accounts for 293 records (57.9%), and calling for 154 records (30.4%). The remaining behaviours comprise 28 fiddling records (5.5%), 17 feeding records (3.4%), 13 nesting records (2.6%) and 1 mating record (0.2%) (Fig. 2).

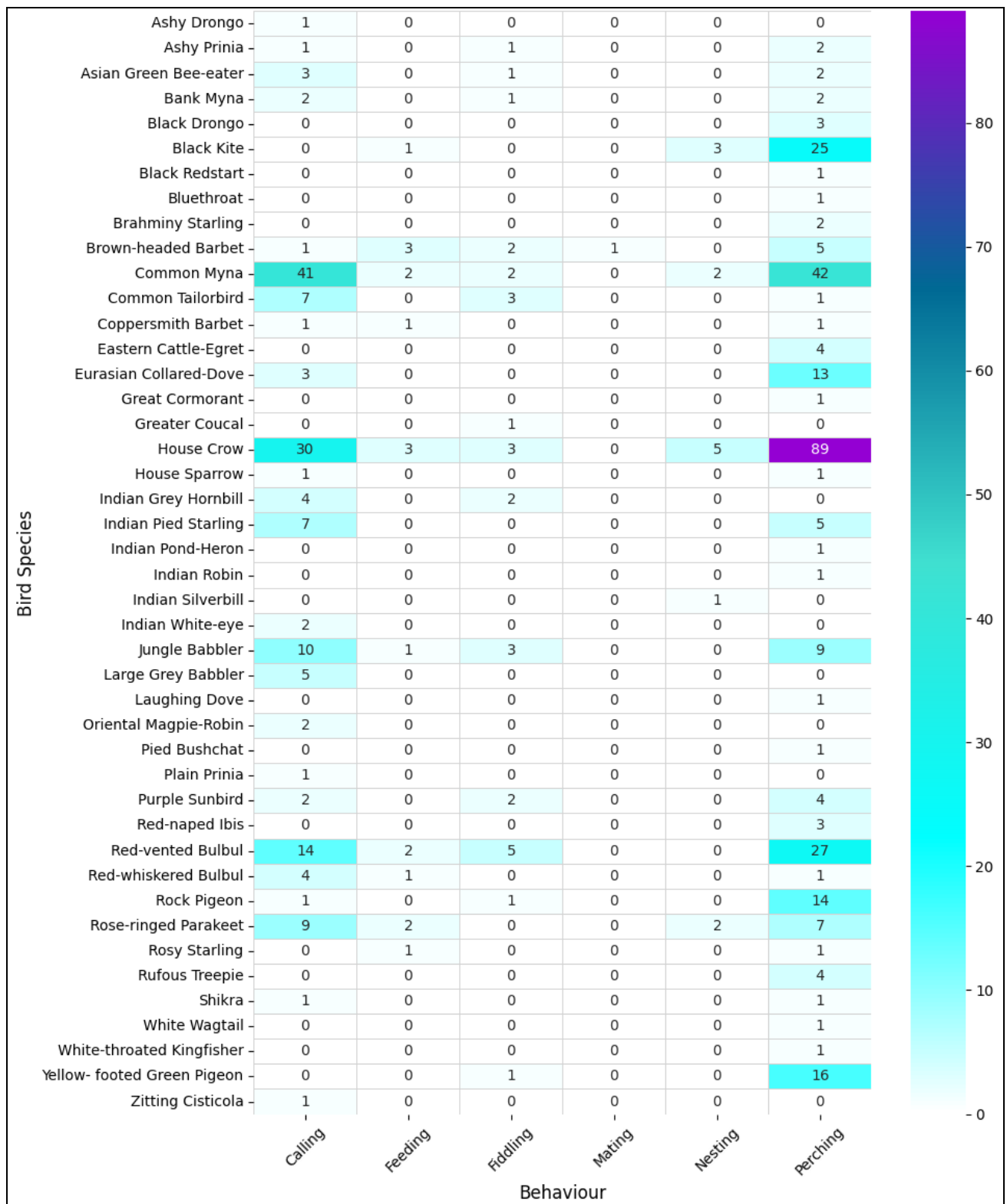


Figure 2: Bird behaviour frequency by species in the dataset.

A small set of bird-behaviour pairs explains most of the activity. The single largest pair is House Crow perching, with 89 records (17.6% of all observations), while House Crow calling contributes another 30 records (5.9%). Common Myna shows an almost even split between perching, with 42 records (8.3%), and calling, with 41 records (8.1%), indicating that its preferred perches double as display posts. Additional high-frequency combinations include

Red-vented Bulbul perching, with 27 records (5.3%), and calling, with 14 records (2.8%); Black Kite perching, with 45 records (4.9%); and perching by three species: Yellow-footed Green Pigeon, with 16 records (3.2%), Rock Pigeon, with 14 records (2.8%), and Eurasian Collared-Dove, with 13 records (2.6%). Two Jungle Babbler pairs: calling, with 10 records (2.0%), and perching, with 9 records (1.8%), plus calling and perching by Rose-ringed Parakeet and calling by Common Tailorbird, with 7-9 records each (1.4-1.8%), complete the list of fifteen pairs that together account for 70% of all interactions (Fig. 2). Behaviours involving direct plant use are infrequent. Feeding events occur mainly in Brown-headed Barbet and House Crow, with 3 records each, and total 17 observations (3.4%). Fiddling, movement among leaves or twigs, peaks in Red-vented Bulbul, with 5 records, but remains marginal overall. Nest-site activity is concentrated in House Crow, with 5 records, and Black Kite, with 3 records, and appears only 13 times in total, while a single mating record (0.2%) involves Brown-headed Barbet (Fig. 2).

3.2. Plant Species Visitor Analysis

Analysis of the plant-centric interaction matrix ($n = 34$ plant taxa) shows a steep gradient in their attractiveness to birds ($n = 44$ bird taxa), with a handful of keystone trees supporting disproportionately large avian assemblages and a long tail of sparsely used ornamentals and exotics. At the apex stands Peepal, which provided resources: fruit, foliage or roosting structure, to 23 bird species, making it the single most connected node in the network. Close behind, Neem hosted 20 species, reflecting both its abundant canopy insects and year-round foliage in Delhi's streetscapes. Two functionally similar but primarily exotic taxa: Vilayati Kikar and Eucalyptus spp., shared third position with 19 visitor species each; their high counts testify to the opportunistic exploitation of fast-growing, drought-tolerant cover despite their non-native status. Sheesham hosted 16 species, underscoring the value of riparian hardwoods even where natural riverine corridors have been narrowed or culverted. Semal attracted 11 species, chiefly during its prolific spring flowering. Pilkhan and Banyan supported 8 and 5 species, respectively, confirming the pan-tropical importance of the genus *Ficus* in sustaining urban wildlife. Other natives in this upper tier included Bakain with 8 species, Saptaparni with 7 and Mulberry with 6, each contributing seasonal fruiting pulses. Widely planted avenue or garden trees such as Katsagon, Karanj, Gulmohar and Jamun each sustained 5-6 bird species, highlighting how diverse planting palettes can broaden foraging options in otherwise built-up grids.

Beyond this point, a substantial drop is evident. Kassod, Subabool, Bougainvillea and Ber each registered 4 visitor species. Ornamental shade trees such as Silver Oak, Ashoka and the introduced Sausage Tree drew 3 species each, suggesting limited but non-negligible ecological utility when woven into mixed plantings. At the lower extreme, Amaltas, Maharukh and Royal Palm supported 2 species each, while ten ornamental or roadside taxa: including Papaya, Kaner, Kadamb, Frangipani, White Frangipani, Chikrassy, Teak, Babool and Weeping Bottlebrush, each recorded only 1 avian associate within the survey window. Although some low counts may reflect seasonal sampling (e.g. off-peak flowering), the consistently sparse use across grids indicates that these ornamentals currently play a minor role in sustaining Delhi's resident bird community (Fig. 3).

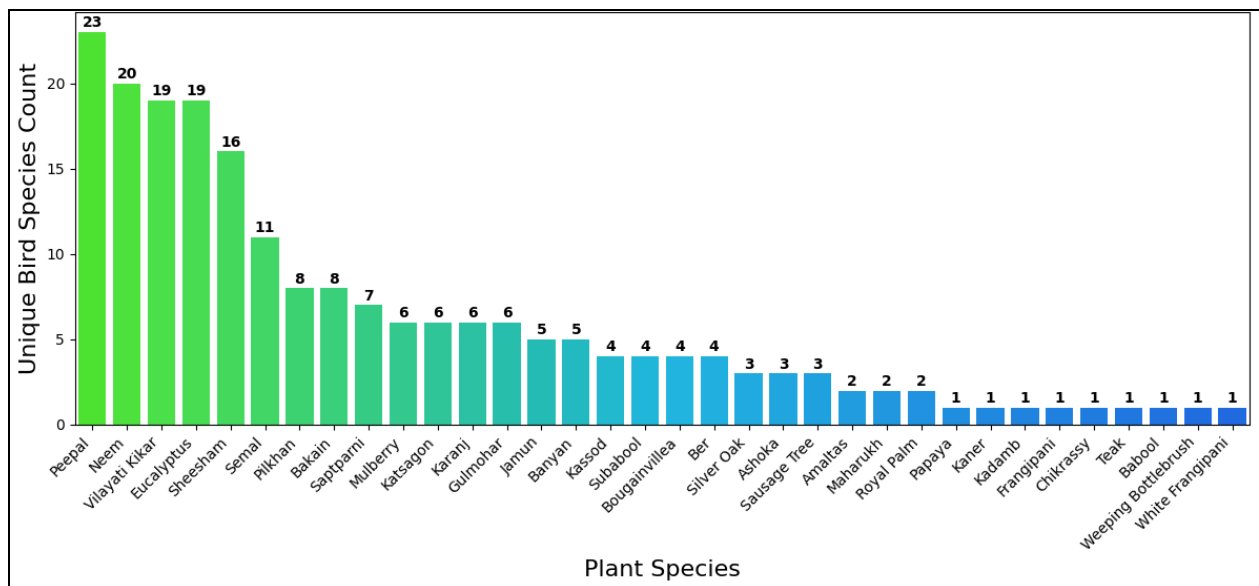


Figure 3: Plant species visited by bird species count

3.3. Strongest Bird-Plant Interactions

The ten strongest bird-plant links, ranked by cumulative bird counts across all grids, illuminate how a small subset of urban-tolerant birds converges on a similarly restricted set of woody hosts, many of them exotic. House Crow foraging or roosting in Eucalyptus groves emerged as the most frequently recorded interaction (57 individuals), underscoring this species' ability to exploit tall, fast-growing exotics that now dominate many avenue plantings. The second-ranked pairing: Rock Pigeon on Vilayati Kikar, with 50 individuals, reveals a comparable synergy between a synanthropic bird and an aggressively invasive tree that offers abundant resting strata in otherwise sparsely vegetated streetscapes. Rock Pigeon also occupied third place in association with Eucalyptus (45 individuals). A more nutritionally driven link appears in the fourth position: Common Myna on Semal, tallying 41 individuals. The profuse spring flowering of Semal furnishes nectar, insects and soft wood, all of which are routinely exploited by mynas. The fifth and sixth pairings returned to the omnipresent House Crow, this time on Neem (37 individuals) and Silver Oak (35 individuals). Rock Pigeon was observed to have a recurrent use of Neem (35 individuals). Asian Green Bee-eater appears twice with Neem (33 individuals) and with Peepal (30) demonstrating how these aerial insectivores track canopy edge habitats rich in flying prey irrespective of the host's native status. House Crow again features in ninth place with Peepal (33), reflecting the fig's year-round fruit and its large boughs suitable for communal roosting (Fig. 4).

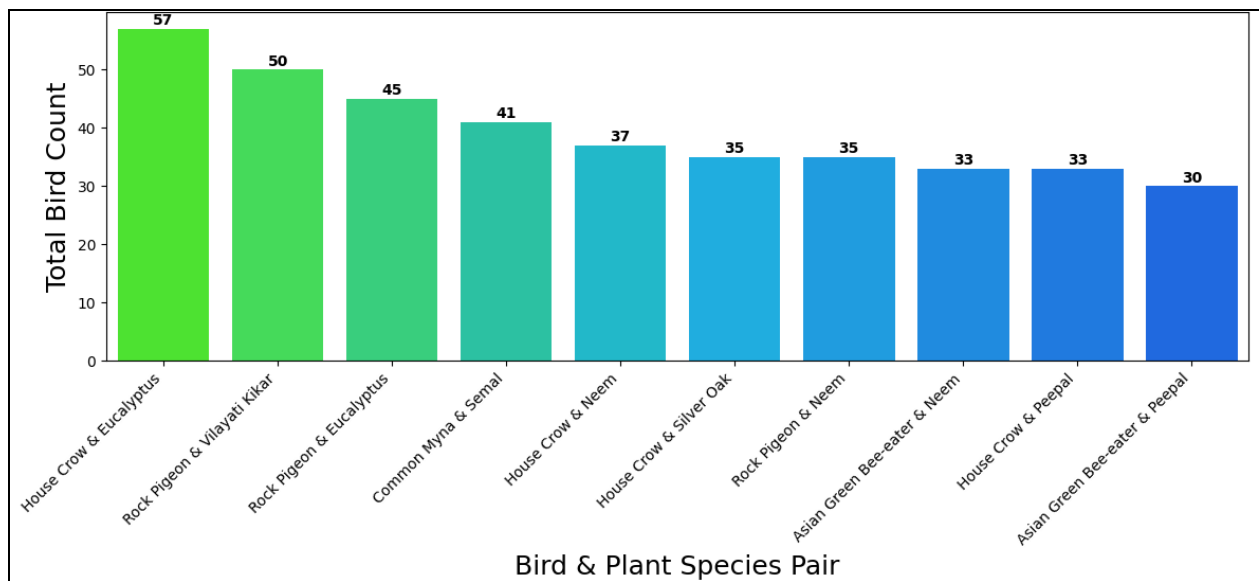


Figure 4: Top 10 strongest bird and plant interaction pairs by total bird count.

3.4. Unique Plant Species visited

The interaction matrix revealed pronounced disparities in the breadth of plant use across the 44 bird species recorded. House Crow topped the spectrum, exploiting 26 distinct plant taxa. Common Myna was nearly as versatile, associating with 23 taxa. A second tier of broad generalists comprised Red-vented Bulbul (14 taxa), Rose-ringed Parakeet (13) and Jungle Babbler (11); each is a common resident that readily shifts between fruiting avenues, ornamental hedges and native groves, and their double-digit tallies reflect that flexibility. In the mid-range, both Rock Pigeon and Black Kite interacted with 9 taxa. Comparable breadth was recorded for Yellow-footed Green-Pigeon and Common Tailorbird, each linked to 8 taxa, and for Brown-headed Barbet, which visited 7. Three species: Eurasian Collared-Dove, Indian Pied Starling and Purple Sunbird, were observed on 6 taxa apiece. The lower-mid segment, with 4 taxa each, included Rufous Treepie, Red-whiskered Bulbul, Ashy Prinia, Indian Grey Hornbill and Bank Myna. Eastern Cattle-Egret, Large Grey Babbler, Coppersmith Barbet and Asian Green Bee-eater each used 3 taxa, representing an even more circumscribed breadth. Species recorded on only 2 taxa, Shikra, Rosy Starling, Brahminy Starling, Black Drongo and Red-naped Ibis, occupied a transitional position between moderate plasticity and single-resource dependence (Fig. 5).

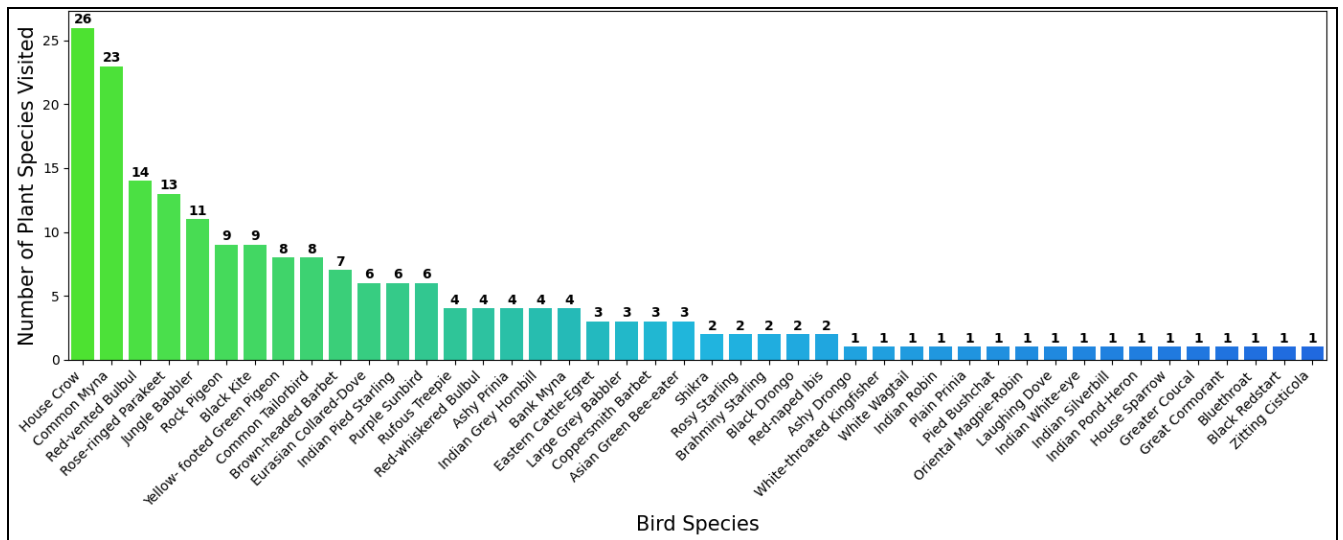


Figure 5: Number of unique plant species visited by each bird species.

Taken together, the data depict a strongly right-skewed distribution of plant use: a small cadre of highly adaptable generalists shoulders the majority of interactions, while fully half of the assemblage exhibits markedly limited plant associations. Such asymmetry is typical of urbanized landscapes where a few winner species capitalize on heterogeneous, human mediated food supplies, whereas many others persist only where preferred plant resources remain intact (Fig. 6).

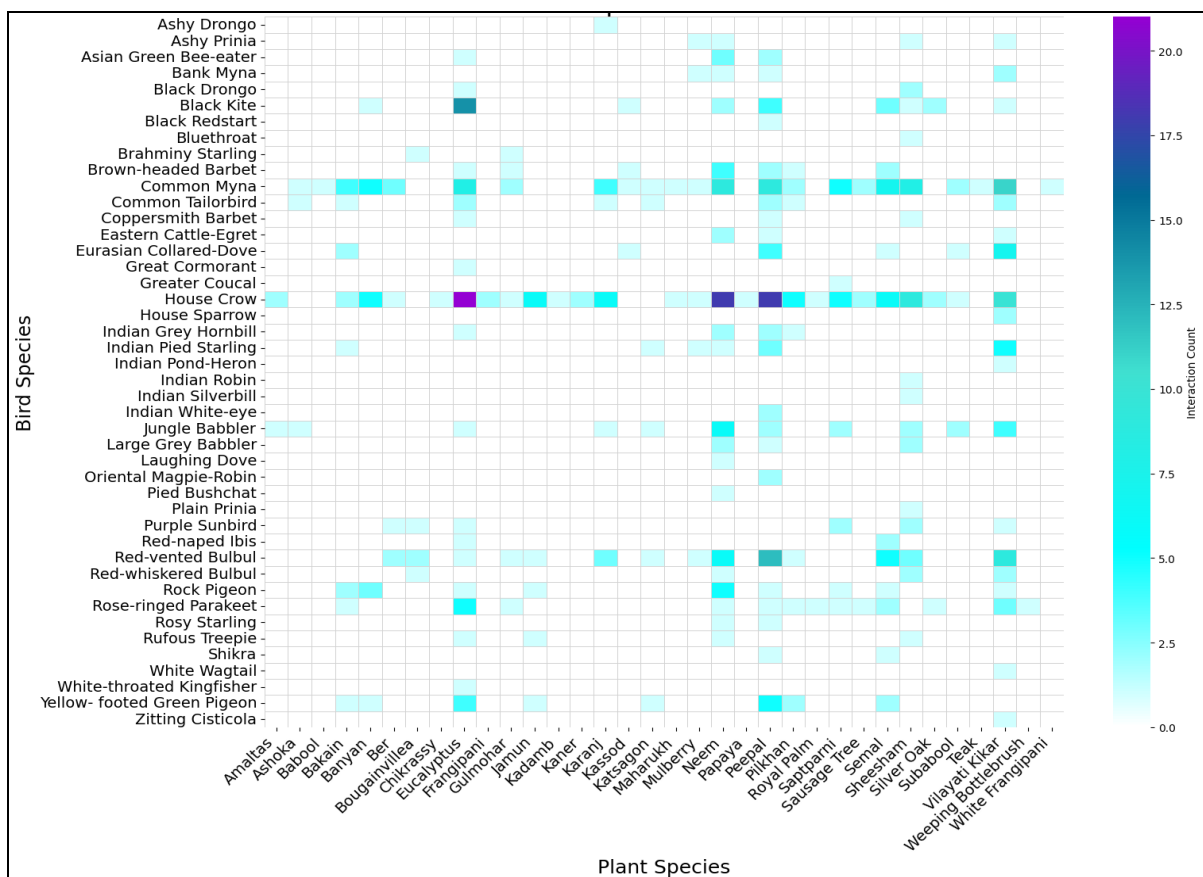


Figure 6: Bird and plant species interaction heat map.

3.5. Pearson Correlation Analyses

Pairwise Pearson correlation coefficients were calculated for bird and plantspecies abundances across the survey grids to quantify the degree of linear co-variation in their spatial distributions. This metric is widely used in community-ecology studies because it (i) enables symmetric, scale-independent comparison of interaction strength among taxa with disparate absolute counts, (ii) captures both positive and negative associations, thereby discriminating potential facilitative links from putative competitive or habitat-segregation patterns, and (iii) remains computationally straightforward, facilitating transparent replication of results. Implementing a minimum-record threshold prior to coefficient estimation further mitigated small-sample bias, ensuring that the derived correlations reflect ecologically substantive patterns rather than artifacts of sparse observations. Collectively, this analytical framework provides a statistically robust and conceptually tractable basis for identifying the most consequential bird-plant pairings and for guiding subsequent multivariate or mechanistic investigations. The python code used for all analyses is provided as a Jupyter notebook in the supplementary material.

3.5.1. Bird- Bird Pearson Correlation

No Threshold

The 44*44 Pearson matrixes divide naturally into four strength classes. Strong positive associations ($r \geq 0.70$) are limited to 79 species pairs: 8% of the 946 unique combinations, but they convey nearly all of the biologically meaningful structure in the data. Within this group, exactly fifteen pairs achieve a perfect correlation of $r = 1.00$: for example, House Sparrow with Indian Pond-Heron, Black Redstart with Indian White-eye, and Bluethroat with Indian Robin. Beyond the perfect set, the upper tail includes Asian Green Bee-eater and Rosy Starling ($r = 0.94$), Eurasian Collared-Dove and Indian Pied Starling (0.93), and Black Kite matched at 0.92 with both Great Cormorant and White-throated Kingfisher. Moderate positive correlations ($0.30 \leq r < 0.70$) encompass 138 pairs, about 15% of the matrix. These coefficients capture looser but still appreciable habitat overlap: Black Kite with Common Myna ($r \approx 0.55$), Ashy Prinia with Purple Sunbird (≈ 0.46), and Bank Myna with Plain Prinia (≈ 0.41). The matrix is dominated by weak or near-zero associations ($-0.29 \leq r < 0.30$), totaling 567 pairs (60%). The mean coefficient in this band is essentially zero (0.02 ± 0.11 SD (Fig. 7A).

Threshold: ≥ 3

Applying the three-records threshold retained 24 bird species, those that occurred in at least three observations, produced 276 pairwise Pearson coefficients. The coefficients span 0.26 to +0.92 and are strongly skewed toward positive values (mean = 0.31, median = 0.30, SD = 0.24). No pair falls below -0.30, confirming that statistically meaningful spatial avoidance is absent at this spatial grain once very rare species are removed. 24 pairs (9% of the matrix) meet or exceed the 0.70 threshold. The highest correlation is observed between Eurasian Collared-Dove and Indian Pied Starling ($r = 0.92$). Other notable dyads include Asian Green Bee-eater with Indian Grey Hornbill (0.92), Bank Myna with Indian Pied Starling (0.90), Eastern Cattle-Egret with Jungle Babbler (0.86), Asian Green Bee-eater with Brown-headed

Barbet (0.84), and Black Kite with Rose-ringed Parakeet (0.81). Several corvid-passerine pairs also register as strong: Common Myna with House Crow (0.80) and House Crow with Indian Grey Hornbill (0.79). A further 129 pairs (47%) fall in the moderate band. Mid-range coefficients (0.55-0.68) repeatedly tie canopy-nesting or cavity-nesting specialists such as Indian Grey Hornbill, Brown-headed Barbet and Red-vented Bulbul to structurally similar companions: Sausage Tree, Bakain and other large crowned trees. Lower-moderate values (0.30-0.55) link generalists (Plain Prinia, Ashy Prinia) to urban-edge associates like Bank Myna and Rosy Starling. The remaining 123 pairs (44%) cluster tightly around zero, with a mean coefficient of 0.05 ± 0.09 SD. Typical examples include Purple Sunbird versus House Crow ($r \approx 0.07$) and Black Drongo versus Rock Pigeon (≈ 0.04). Because these values are small and evenly distributed, they indicate that most retained species vary independently once extremely infrequent co-occurrences are excluded. The lowest coefficient, Ashy Prinia versus Black Kite (-0.26), remains far above the -0.50 threshold usually interpreted as evidence of active segregation (Fig. 7B).

Threshold: ≥ 5

After limiting the analysis to species recorded in at least five observations, the bird-bird matrix contains 18 species and all 153 pairwise Pearson coefficients. Values extend from -0.29 to 0.93, with a mean of 0.37 and a median of 0.41, showing a clear tilt toward positive co-occurrence. Standard deviation is 0.27, so most coefficients cluster within roughly a quarter-unit of the mean and only a small fraction approach the extremes. Fifteen pairs exceed the strong-association threshold of 0.70. The tightest link joins Eurasian Collared-Dove and Indian Pied Starling with a coefficient of 0.93, indicating that these two species occupy almost the same habitats. Asian Green Bee-eater and Indian Grey Hornbill follow at 0.92, Bank Myna and Indian Pied Starling at 0.90, and Asian Green Bee-eater with Brown-headed Barbet at 0.86. A value of 0.82 couples Brown-headed Barbet with Indian Grey Hornbill, while Black Kite pairs with Rose-ringed Parakeet at 0.82. Common Myna aligns with House Crow at 0.79, House Crow with Indian Grey Hornbill at 0.79, and Asian Green Bee-eater with House Crow at 0.78. Remaining strong links include Bank Myna with Eurasian Collared-Dove at 0.77, Indian Pied Starling with Red-vented Bulbul at 0.76, Black Kite with House Crow at 0.73, Bank Myna with Red-vented Bulbul at 0.73 and Eurasian Collared-Dove with Red-vented Bulbul at 0.73. 73 coefficients fall in the moderate band between 0.30 and 0.69. The upper part of this range includes Black Kite with Yellow-footed Green Pigeon at 0.69, Common Myna with Jungle Babbler at 0.69, Asian Green Bee-eater with Jungle Babbler at 0.68 and Asian Green Bee-eater with Rock Pigeon at 0.68. Coefficients near 0.65 link Common Tailorbird with Yellow-footed Green Pigeon, Jungle Babbler with Large Grey Babbler and Brown-headed Barbet with House Crow. 65 pairs are weak or near-zero, lying between minus 0.29 and plus 0.29. The average within this band is 0.05 with a spread of 0.09, indicating that once rare species are excluded, most birds vary independently across the grids. No coefficient breaches that negative threshold, so meaningful avoidance is absent at this scale (Fig. 7C).

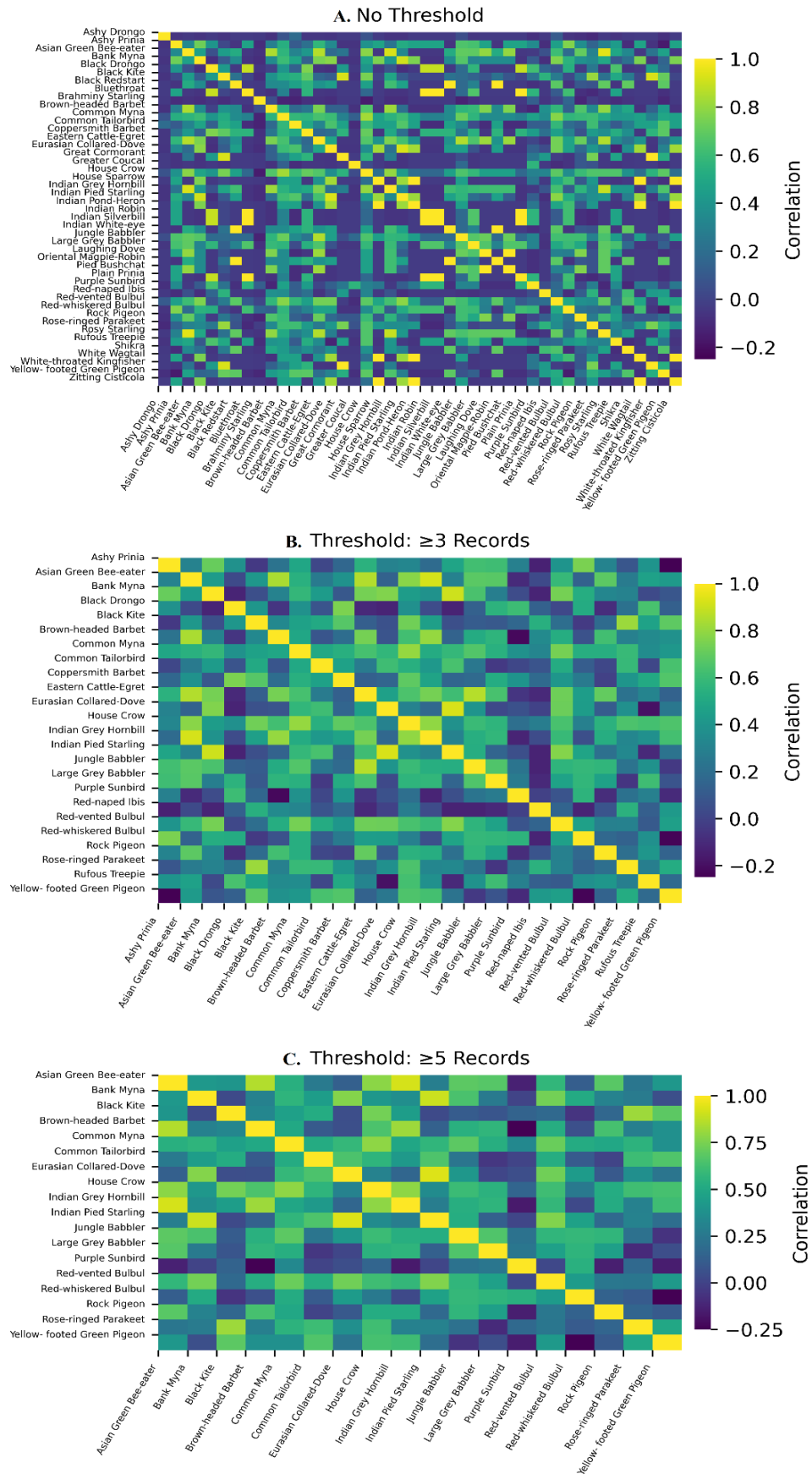


Figure 7: Bird-Bird correlation for all three thresholds.

3.5.2. Plant-Plant Pearson Correlation

No Threshold

The plant-plant correlation matrix, calculated for 34 species, contains 561 unique Pearson coefficients ranging from -0.12 to +1.00. The distribution is markedly skewed to the positive side (mean = 0.46, median = 0.51, SD = 0.31), indicating that most species tend to co-occur rather than segregate at this spatial grain. A small but ecologically revealing upper tail comprises 18 strongly positive pairs ($r \geq 0.95$; 3.2% of all combinations). Thirteen of these are perfect ($r = 1.00$). The first clique links Babool, Teak, and White Frangipani. The second, larger clique joins the ornamentals Chikrassy, Frangipani, Kadamb, Kaner and Papaya. Five additional very high coefficients ($r \approx 0.95$) bridge this ornamental cluster to Jamun. Below this threshold lie 266 moderate positive correlations ($0.50 \leq r < 0.95$; 47% of the matrix). Coefficients in the 0.70-0.90 range typically connect Banyan with Bakain, and Bougainvillea and Kaner with Babool. Values between 0.50 and 0.70 links Eucalyptus and Jamun to several less common companions. The bulk of the matrix: 275 pairs (49%), falls in a weak or near-zero band ($-0.10 < r < 0.50$). Here, coefficients cluster tightly around zero. Only two pairs show even modest negative association (Bakain versus Bougainvillea and Katsagon versus Silver Oak, $r \approx -0.12$), far from the conventional 0.50 threshold that would signal competitive exclusion; negative structure is therefore negligible at the grid scale (Fig. 8A).

Threshold: ≥ 3

After imposing the ≥ 3 records filter, the plant dataset is reduced to 23 species occurring in at least three observations each. Their pair wise matrix now contains 253 Pearson coefficients, spanning -0.21 to +0.92 and strongly biased toward positive values (mean = 0.47, median = 0.51, SD = 0.28). No perfect ($r = 1.00$) matches remain, confirming that the threshold successfully removed results driven by single-site coincidences. Strong co-occurrence ($r \geq 0.70$) is still prominent: 63 pairs, or one quarter of the matrix, exceed this cut-off. Karanj aligns almost perfectly with Peepal ($r = 0.92$), Sheesham (0.91) and Neem (0.90). Exotic avenue trees also cluster tightly: Eucalyptus with Silver Oak (0.90), while mature shade assemblages link Saptparni simultaneously to Sausage Tree (0.89), Sheesham (0.88) and Banyan (0.85). Moderate positive associations ($0.30 \leq r < 0.70$) account for 116 pairs (46%). Jamun pairs at $r \approx 0.63$ with Peepal and Neem, and Bougainvillea groups at 0.50-0.65 with Subabool and Vilayati Kikar. Weak or near-zero correlations ($-0.10 < r < 0.30$) make up 74 pairs (29%). Here, species co-occur too erratically for any pattern to emerge once rarity is discounted; for instance, Ashoka and Sheesham register $r \approx 0.04$. Negative links are both scarce and mild, only 20 coefficients fall below zero, the lowest being Katsagon (*Pterocarpus marsupium*) against Silver Oak at $r \approx -0.21$. Even these negative tails remain far above the -0.50 threshold for meaningful spatial segregation, underscoring that competitive exclusion among tree species is negligible at the 6.25 km² grid scale (Fig. 8B).

Threshold: ≥ 5

Imposing the five-record threshold retains 20 tree species and generates 190 Pearson coefficients. The coefficients extend from -0.302 to 0.920, average 0.503 with a standard deviation of 0.284, and the median is 0.570, confirming a strong overall tendency for the

species to co-occur rather than segregate at the scale. Positive structure is especially pronounced: fifty-six pairs, just under thirty per cent of the matrix, reach or exceed the strong-association benchmark of 0.70, whereas only a single pair: Katsagon with Silver Oak at minus 0.302 falls into the negative domain. The tightest link couples Karanj with Peepal at 0.920 and is matched almost exactly by Karanj with Sheesham at 0.919. Eucalyptus aligns with Silver Oak at 0.900, Karanj matches Neem at 0.899, and Saptparni pairs with Sheesham at 0.891 and with Sausage Tree at 0.887. Old-growth shade trees contribute several further high values: Peepal relates with Semal at 0.850, Jamun joins Pilkhan at 0.850, Neem again joins Sheesham at 0.850, and Gulmohar joins Semal at 0.850. Moderate positive associations, defined here as coefficients from 0.30 up to 0.69, account for 87 additional pairs. Typical examples are Jamun with Neem at 0.622, Pilkhan with Banyan at 0.605, and Bougainvillea with Neem at 0.566. 46 pairs lie in the weak or near-zero band between -0.30 and 0.30. The average within this class is roughly 0.070. Bakain with Bougainvillea illustrates the low end at minus 0.300, whereas Ashoka with Sheesham registers 0.040 near the centre of the distribution. The dataset, therefore, contains a distinct, management-driven stratum of 56 strongly co-occurring pairs, a broader but weaker layer of moderately positive links, and virtually no evidence of competitive exclusion (Fig. 8C).

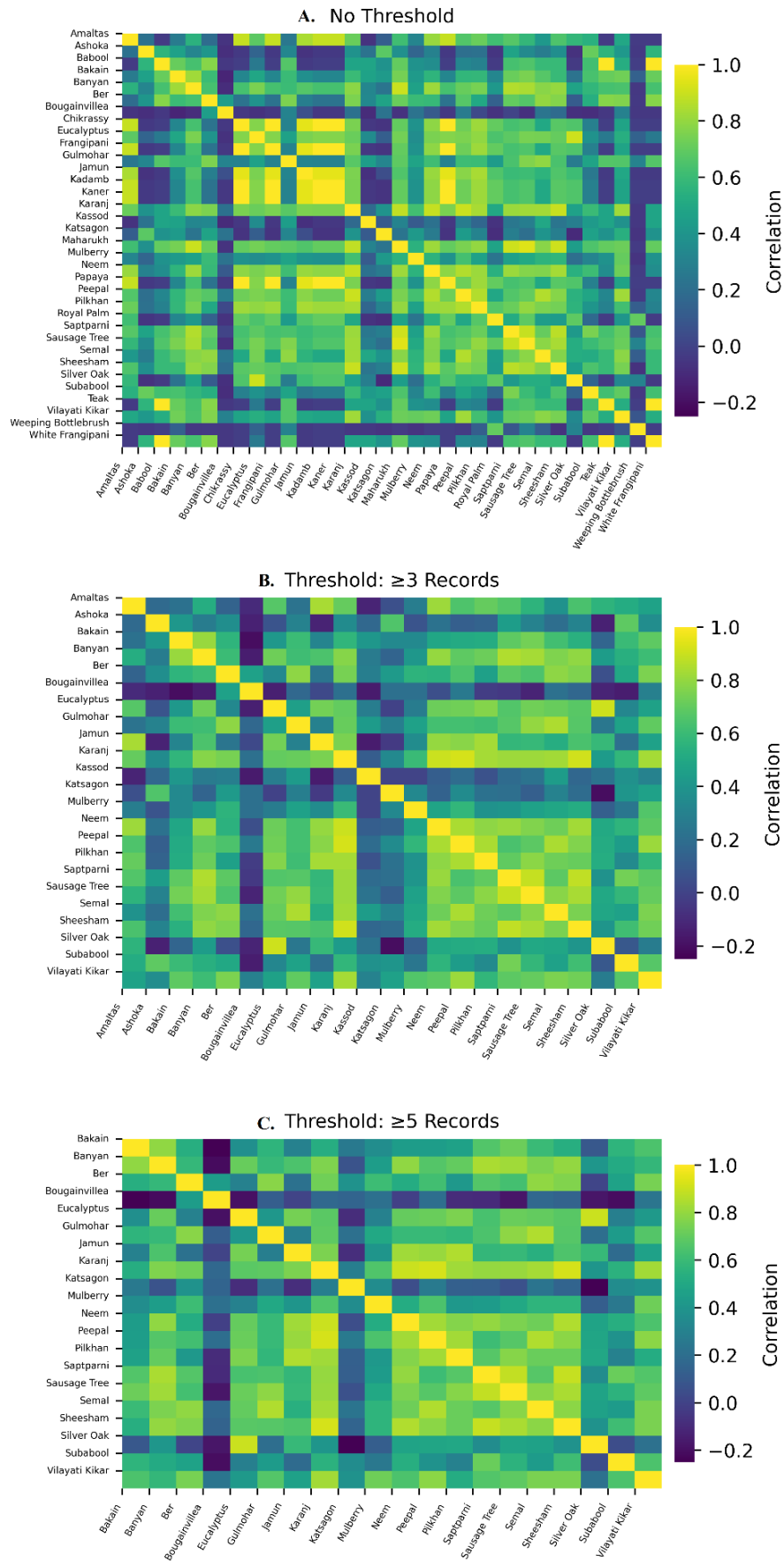


Figure 8: Plant-Plant Pearson correlation heatmap for all three thresholds

3.5.3. Bird-Plant Pearson Correlation

No Threshold

The bird-plant cross-correlation matrix links 44 bird species with 34 plant taxa, yielding 1496 Pearson coefficients that range from -0.14 to +1.00 (mean = 0.03, median $\approx$ -0.02, SD = 0.13). The distribution is sharply peaked around zero, but a narrow positive tail contains the few biologically interpretable links. Eight pairs (0.5% of all combinations) reach $r \geq 0.70$. One is perfect: Indian Pond-Heron and Papaya ($r = 1.00$). The remaining high-end links span $r = 0.70$ -0.78. Brahminy Starling with Gulmohar (0.77), Black Redstart with Silver Oak (0.75), Red-whiskered Bulbul with Frangipani (0.71), Indian Grey Hornbill with Maharukh (0.71), Greater Coucal with Kaner (0.70), Oriental Magpie-Robin with Kassod (0.70) and House Sparrow once more with Papaya (0.70). All involve fleshy fruit, sheltered understorey, or rich arthropod prey, suggesting shared micro-habitat rather than direct facilitation. Seventy-five additional pairs fall in the moderate positive band ($0.30 \leq r < 0.70$). The strongest of these links canopy-nesting or cavity-nesting birds to large, architecturally complex trees: Indian Grey Hornbill (0.68) and Brown-headed Barbet (0.67) both peak with the Sausage Tree, while Indian Pied Starling matches Bakain at 0.67. Mid-range coefficients (0.55-0.60) bind species such as Indian Pond-Heron and House Sparrow to Vilayati Kikar, and passerines: Rosy Starling, Plain Prinia, Bluethroat, to Sheesham and Silver Oak. Slightly lower but still notable links pair Rose-ringed Parakeet with both Royal Palm (0.58) and Frangipani (0.67). Weak or near-zero correlations ($-0.30 < r < 0.30$) dominate the matrix, accounting for 1413 pairs (94%) (Fig. 9A).

Threshold: ≥ 3

Applying the three-record filter yields a bird-plant matrix with 552 coefficients for 24 bird species and 23 tree taxa. Values run from -0.14 to 0.68, cluster tightly around zero (average 0.053, standard deviation 0.14) and show no evidence of strong negative association. Although no pair reaches the strong-link threshold of 0.70, thirty-seven combinations sit in the moderate zone between 0.30 and 0.68 and therefore merit attention. The single highest coefficient, 0.68, ties Indian Grey Hornbill to Sausage Tree, a cavity-rich species whose large pods and broad canopy evidently attract repeated use by this specialized frugivore. Brown-headed Barbet shows a nearly equal affinity for the same tree, registering 0.67, and Indian Pied Starling aligns most closely with Bakain at 0.67. Other notably high pairs include Indian Grey Hornbill with Neem at 0.61 and Rock Pigeon with Banyan at 0.54, pointing to tall, old-growth trees that provide both shelter and food resources. Two Rose-ringed Parakeet links stand out: Amaltas scores 0.47 and Eucalyptus 0.45. Ashy Prinia joins Mulberry at 0.46, while Red-naped Ibis pairs with Gulmohar at 0.43. Black Kite and Kassod yield 0.43 and Red-whiskered Bulbul reaches 0.43 with Vilayati Kikar. The remaining moderate coefficients fall between 0.30 and 0.42. Examples include Bank Myna with Ashoka at 0.42, Large Grey Babbler with Sheesham at 0.42, and House Crow with Eucalyptus at 0.36; Common Myna shows a consistent but weaker signal with Neem at 0.36, Eucalyptus at 0.36 and Peepal at 0.35. Eurasian Collared-Dove matches Peepal at 0.33, while Common Tailorbird aligns with Bakain at 0.32. All other bird-plant pair's exhibit coefficients below 0.30 in absolute

magnitude, indicating statistical independence at the 6 km² grid scale. The lowest value, -0.14, links Eurasian Collared-Dove to Sheesham and is far removed from the -0.50 benchmark for meaningful spatial segregation (Fig. 9B).

Threshold: ≥ 5

Filtering the cross-taxon matrix to species recorded in at least five observations leaves 18 birds, 20 tree species, and 360 bird-plant pairs. Pearson coefficients extend from -0.14 to 0.68, cluster tightly around zero (mean 0.07, median 0.03, standard deviation 0.14) and show no evidence of strong negative association. Only five links exceed the mid-level mark of 0.50: Indian Grey Hornbill with Sausage Tree scores 0.68, Brown-headed Barbet with the same tree 0.67, Indian Pied Starling with Bakain 0.67, Indian Grey Hornbill with Neem 0.61 and Rock Pigeon with Banyan 0.54. 24 additional pairs lie in the softer positive band between 0.30 and 0.49; the upper edge of this group includes Rose-ringed Parakeet with Eucalyptus at 0.45, Brown-headed Barbet with Neem at 0.44, Red-whiskered Bulbul with Vilayati Kikar at 0.42, Large Grey Babbler with Sheesham at 0.42 and House Crow with Sausage Tree also at 0.42. The remaining 331 coefficients fall between -0.14 and 0.29, confirming statistical independence for the vast majority of bird-tree combinations. The weakest value, -0.14, links Eurasian Collared-Dove to Sheesham and is far above the conventional -0.50 threshold used to flag spatial segregation (Fig. 9C).

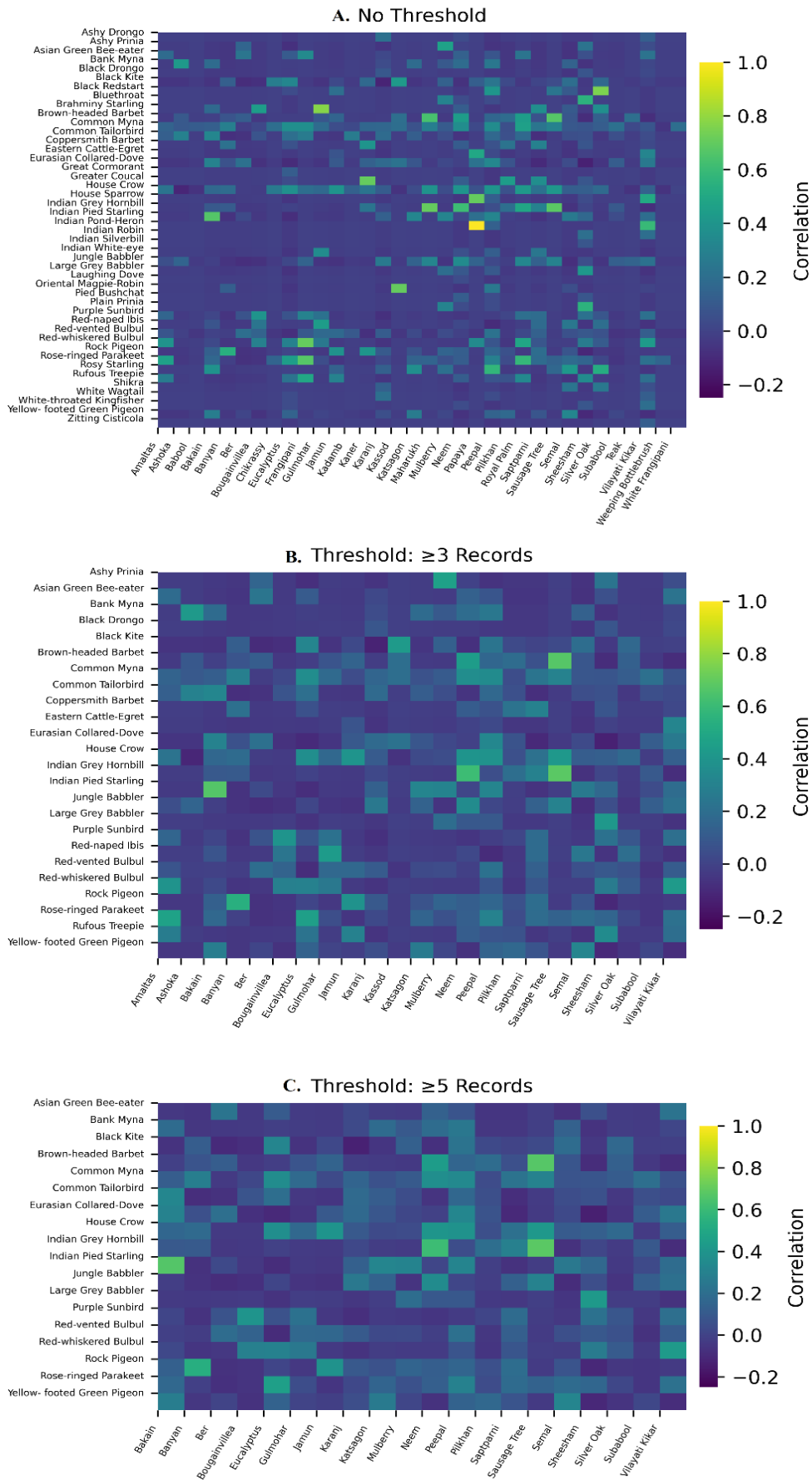


Figure 9: Bird-Plant Pearson correlation heatmap for all three thresholds.

4. Discussion

The ongoing removal and pruning of Vilayati Kikar (*Prosopis juliflora*) in Delhi's urban forests is driven by evidence that invasive-dominated stands can depress overall biodiversity. For instance, areas with very high Vilayati Kikar density in semi-arid India support lower bird richness and lose many sensitive species, retaining mostly generalist birds like pigeons and sparrows. Our study confirms that the tree currently provides important structural habitat for several urban birds - we recorded synanthropic species such as the Rock Pigeon extensively using Vilayati Kikar for roosting and territorial calls (Choudhary & Chishty, 2020; Johnston, 2024; Khera et al., 2009). House Sparrows and Indian Pond-Herons also showed strong positive associations with this invasive tree in our surveys (Rawal et al., 2021; Skórka et al., 2016). These observations raise concerns that aggressive canopy pruning of Vilayati Kikar, if not carefully managed, could temporarily diminish perching and calling opportunities for these birds. In the absence of equally functional native replacements, birds may be forced to shift their ranging and behaviour, potentially vacating pruned areas until alternative foliage matures (Hanle et al., 2020). To mitigate such impacts, we recommend a staggered pruning schedule and adaptive management approach. Restoration programs should be phased in space and time so that some stands of Vilayati Kikar (or their canopy structure) are retained while new native saplings establish, thereby providing continuous habitat for birds during the transition (O'Leary et al., 2021).

Concurrently, behaviour-based monitoring should be integrated into the project: birds are rapid indicators of habitat change (O'Leary et al., 2021) and tracking their perch use, calling behaviour, and site fidelity can reveal if the pruned areas continue to meet their ecological needs. If significant declines in bird activity are observed post-pruning, management should adjust by, for example, slowing the removal rate or enhancing habitat structure (e.g., installing perching poles or conserving select old trees as “framework” species) (Cavallero et al., 2013).

However, without lush crowns, those pruned trees offer only limited bird support until native saplings grow tall. In summary, urban forest restoration must balance invasive species control with wildlife habitat preservation. Delhi's Vilayati Kikar initiative provides a test case for bird-friendly invasive management in cities. Our evidence suggests that maintaining a patchwork of old and new growth - rather than indiscriminate clearance - would allow urban bird communities to adjust gradually. By adopting staggered canopy reduction, rigorous avian monitoring, and expedited native replantation, city planners can ensure that the ecological functions of urban trees as perches, song posts, and refuges remain intact.

For urban planners, our results translate into three concrete design principles. First, restoration of the Central Ridge and biodiversity parks should prioritise structurally complex native keystone trees such as *Ficus* spp., Neem and Sheesham, which support the richest and most behaviourally diverse bird assemblages across the city. Second, street-tree and park planting schemes should avoid monotonous rows of low-value ornamentals and instead use mixed palettes that combine drought-tolerant natives with a limited number of non-native but structurally useful species, thereby spreading foraging and roosting opportunities through the urban fabric. Third, invasive-tree removal plans need to be scheduled in space and time so that at any point along the Ridge and in major green corridors, birds can shift between overlapping patches of old crowns and maturing native plantings rather than facing abrupt

structural gaps. Such measures will help safeguard Delhi's rich bird life through the current transition, validating the principle that urban biodiversity conservation should proceed hand-in-hand with greening initiatives.

A small set of ecologically versatile natives (notably Neem) and hardy exotics (Eucalyptus) forms the structural backbone of bird-plant interactions in the metropolis, whereas many ornamentals contribute little beyond aesthetic value. Prioritising the retention and strategic planting of high-value keystone trees, alongside diversifying mid-tier native species, should therefore be central to any habitat-enhancement scheme aimed at bolstering avian functional diversity in rapidly urbanising landscapes. Structurally or trophically important trees: Sausage Tree, Bakain, Neem, Banyan, Amaltas, Eucalyptus, Mulberry, Gulmohar, Kassod, Ashoka, Sheesham and Peepal, consistently elevate local occupancy for hornbills, barbets, starlings, pigeons, parakeets, prinias, ibises and several urban generalists (Kitamura, 2011; Wagh et al., 2025). For Rufous Treepie, Ashy Prinia, Indian Grey Hornbill, and Bank Myna, plant associations appear broad enough to permit diet switching yet sufficiently bounded to suggest preferential targeting of certain fruiting or flowering phenologies (Patel, 2012; Wagh et al., 2025). House Crow and Common Myna are two of Delhi's most behaviourally plastic inhabitants, due to their abundance and association with many tree species (Kaur, 2020; Patel, 2012). Taken together, just three bird species: House Crow, Rock Pigeon, Asian Green Bee-eater and four tree taxa: Eucalyptus, Vilayati Kikar, Neem and Peepal, account for eight of the ten highest-volume interactions. This clustering highlights an urban network in which ecological generalists repeatedly capitalise on fast-growing exotics and a handful of native keystone trees. Such redundancy may buffer these birds against habitat change, yet it simultaneously signals a functional bottleneck: if management reduces the prevalence of these particular hosts, a large fraction of observed bird activity could be displaced, with uncertain consequences for less plastic species that share the same sites.

Thresholding at three records removes spurious perfect correlations generated by single-grid coincidences and sharpens the ecological signal: strong positive links now involve common, behaviourally compatible species rather than rare outliers. The high- r pairs provide a concise set of guild indicators: open-field insectivores (Asian Green Bee-eater-Brown-headed Barbet), wetland scavengers (Black Kite-Rose-ringed Parakeet) (Kumar et al., 2014; Shiels & Kalodimos, 2019), and peri-urban granivores (Eurasian Collared-Dove-Indian Pied Starling), that can anchor joint-species occupancy or network analyses. Finally, the prevalence of weak correlations ensures that multicollinearity remains low when species are modelled individually, reinforcing the inference that habitat structure, rather than inter-specific competition, dominates bird assemblage patterns in Delhi's urban landscape once a minimal co-occurrence criterion is imposed (Shaw et al., 2024).

The observed patterns of bird-tree interactions in Delhi align closely with global research emphasising the importance of habitat complexity and structural diversity for urban avian communities (Carrasco et al., 2019; Goetz et al., 2007; Hanle et al., 2020; Shaw et al., 2024). The dominance of perching and calling behaviours reflects how urban trees primarily function as three-dimensional habitat structures that expand vertical space availability, supporting the principle that polyculture and agroforestry farming improve habitat complexity, habitat heterogeneity (e.g., tree species richness), and microclimate regulation (Yahya et al., 2022).

The concentration of feeding activities among frugivorous species like Brown-headed Barbet supports research demonstrating that multiple tree species or polyculture farming practice can benefit birds and other biodiversity by providing considerable resources (e.g., food, prey availability, and shelter), therefore, improving foraging and nesting opportunities compared to monoculture plantations (Ragusa-Netto, 2002; Yahya et al., 2022). This pattern validates the importance of maintaining diverse native tree assemblages that provide complementary resources across different seasons and ecological requirements (Hanle et al., 2020). The preference for larger, more structurally complex trees reflects their function as 'keystone structures' because of their disproportionate role in the ecosystem relative to the area occupied (Pustkowiak et al., 2021; Rottenborn, 2024). This principle applies directly to urban conservation strategies, where protecting large mature trees can yield conservation benefits far exceeding their spatial footprint (Wagh et al., 2025).

The relationship between tree characteristics and bird utilisation patterns supports research indicating that increasing tree girth, cover, and crown size may enhance seedling recruitment (Wang et al., 2022). The trees most valuable for bird habitats also contribute to long-term ecosystem regeneration through seed dispersal and recruitment facilitation, creating positive feedback loops essential for urban biodiversity persistence (Coates-Estrada & Estrada, 1986; Kinnaird et al., 2024; Kitamura, 2011). However, the data also reflect the complex trade-offs inherent in urban tree-bird relationships (Vincze et al., 2016). The research acknowledges that trees may increase predation risk for some species while benefiting others (Depalma & Mermoz, 2019) reminds us that urban forest management must consider diverse species requirements and potential ecological conflicts. The correlation patterns observed in Delhi, showing management-driven rather than purely ecological associations between birds and trees, highlight how human landscape design decisions mediate urban biodiversity patterns (Rawal et al., 2021). This finding underscores the critical importance of evidence-based urban forestry that incorporates ecological principles into planning decisions (Shaw et al., 2024).

For Delhi and similar megacities, the evidence supports prioritising diverse native tree plantings that provide the habitat complexity, habitat heterogeneity (e.g., tree species richness), and microclimate regulation (Yahya et al., 2022) essential for supporting urban bird communities. The research validates strategies that protect existing large trees while establishing new plantings that create the structural stratification and resource diversity necessary for sustaining avian biodiversity in rapidly urbanising landscapes (Hanle et al., 2020; Rottenborn, 2024). These findings contribute to growing recognition that urban areas can serve as critical refugia for biodiversity when properly designed and managed, with tree-bird interactions serving as both indicators of ecosystem health and drivers of ecological resilience in urban environments (Gonji et al., 2024; Rawal et al., 2021).

5. Conclusion

Urban tree-bird interaction networks play a critical role in maintaining ecological resilience in megacities. This study shows that habitat complexity offered by trees, particularly native keystone species, is essential for sustaining urban avifauna. While invasive trees such as *Prosopis juliflora* currently provide important structural habitat for several bird species, their control must be implemented through adaptive, phased management that maintains functional

habitat continuity. Preserving a diverse array of tree species, both native and exotic, while prioritizing structurally complex native keystones will best support urban bird communities during large-scale restoration initiatives. Taken together, these findings situate Delhi's bird-tree interaction network at the nexus of biodiversity conservation, invasive species control and climate resilient urban greening. By demonstrating how a small set of native keystone trees and structurally dominant invasive underpin the city's avifauna, the study highlights both the risks of uncoordinated canopy removal and the opportunities for informed restoration design. Embedding such species level ecological information into Ridge restoration plans, biodiversity park layouts, and street tree policies can help Delhi reconcile invasive tree management with the long-term maintenance of urban biodiversity and associated ecosystem services.

Declaration of Conflict of Interest

The authors declare that they have no known conflict of interests.

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