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Native fauna interact differently with native and alien trees in a tropical megacity

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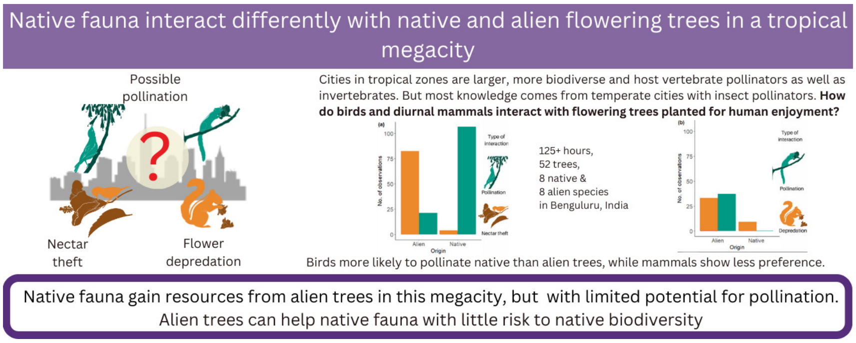
HIGHLIGHTS

- Despite tropical regions hosting the largest cities in the world, limited literature in urban ecology focuses on cities here
- In Bengaluru, India, alien trees can provide local fauna with resources that have otherwise been lost to rapid urbanisation.
- Diurnal avian pollinators are more likely to pollinate native species but this is affected by tree species.
- Diurnal mammals are more likely to depredate the flowers of native trees and pollinate alien trees.

GRAPHICAL ABSTRACT


Native fauna interact differently with native and alien flowering trees in a tropical megacity

Cities in tropical zones are larger, more biodiverse and host vertebrate pollinators as well as invertebrates. But most knowledge comes from temperate cities with insect pollinators. **How do birds and diurnal mammals interact with flowering trees planted for human enjoyment?**

125+ hours,
52 trees,
8 native &
8 alien species
in Benguluru, India

Birds more likely to pollinate native than alien trees, while mammals show less preference.

Native fauna gain resources from alien trees in this megacity, but with limited potential for pollination. Alien trees can help native fauna with little risk to native biodiversity

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ABSTRACT

The negative effects of invasive alien plant species on natural ecosystems are well known. However, in rapidly growing cities, alien plants can provide native fauna with resources otherwise lost due to the biotic homogenization, which is common to urban ecosystems. Interactions of native fauna with alien flora have thus far focused largely on invertebrate pollinators in temperate cities in the northern hemisphere. Cities in tropical areas, however, are larger and are growing more rapidly, and host a variety of vertebrate pollinators. Understanding how birds and mammals interact with native and alien flora in these megacities could improve management of urban ecosystems in highly biodiverse regions while limiting invasion potential. Therefore, here we investigate whether native diurnal birds and mammals interact differently with native versus alien trees in Bengaluru, India where historical planting has led to an abundance of alien tree species. We find that tree origin alone was not an important predictor for bird species richness and abundance, but taller native trees with large floral display sizes were more species rich than alien trees of similar floral displays. As expected from their shared evolutionary history, nectarivorous birds fed from native trees more often in a manner that could facilitate pollination, but engaged in nectar theft more often with alien trees. Squirrels (the mammal observed most frequently to interact with flowers) were more likely, however, to depredate flowers of native trees. Our results suggest alien trees can be an important resource for fauna in expanding urban areas, and that nectar theft by birds could reduce the seed set of alien trees.

1. Introduction

Many of the >17,000 plant and animal species recognised as established aliens (Seebens et al., 2017) are invasive and have detrimental impacts on

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ecosystems (Emer et al., 2016). Understandably perhaps, research efforts have focused on these invasive species, but this bias has resulted in alien species which are not classified as harmful invasives often being vilified. Alien species, however, may also have neutral (e.g. by replacing recently lost species from existing niches) or even positive impacts on ecological communities. For example, urban areas are hotspots for both intentional and unintentional introductions of alien species (Vitousek et al., 1996). Here, suboptimal conditions for native species can result in replacement by alien species (Cadotte et al., 2017), or alien species can provide novel resources that support the persistence of native species. When this involves species interactions such as pollination or seed dispersal, this can then facilitate the spread of alien species outside of urban areas (Von Der Lippe et al., 2005). Despite the potential importance of native and alien species interactions in urban areas, however, the role of alien species in urban ecosystems is only just beginning to be explored (Cadotte et al., 2017). Addressing this knowledge gap is crucial as cities expand and urban land cover continues to increase exponentially (Glaeser and Kahn, 2004).

A major concern with urbanization is biotic homogenization (McKinney, 2006) through direct [e.g. land modification (Marzluff, 2001)] and indirect [e.g. unintentional transportation of alien species via human activities (Brown and Sax, 2004)] effects. However, there is a growing awareness that alien species may also have positive effects on native fauna and flora. For example, along with outcompeting native species or altering nutrient cycling (Waller et al., 2020), in some cases alien species can facilitate native species through mechanisms like habitat modification, trophic subsidy, competitive and predatory release, and by enhancing pollination and dispersal services (Rodriguez, 2006). In urban habitats where there is a loss of native species, it is possible that alien species could offset biotic homogenization (Von Der Lippe et al., 2005). For example, native butterflies in urban areas of California are entirely dependent on alien host plant species (Shapiro, 2002). A similar argument is currently being debated for natural environments, with keystone species-replacement in rewilding schemes suggested to mitigate the loss of function previously provided by extinct or extirpated species (Corlett, 2016; Hansen, 2010). However, investigations into how native species utilise alien species in urban centers are limited (Cadotte et al., 2017).

Pollinator-plant networks provide an ideal system to investigate potential ‘urban rewilding’, or the offset of biotic homogenization through facilitation of native species interactions. Pollination and seed dispersal are key processes in plant regeneration (Neuschulz et al., 2016), yet stable networks of plants and mutualists can be vulnerable to the introduction of new species (Bartomeus et al., 2008). A subsequent loss of pollinators and seed dispersers can have cascading effects on the urban ecosystem (Anderson et al., 2011). Plant-pollinator interactions, which are more specialised than plant- seed disperser interactions (Jordano, 1987), are less frequently studied. However, despite being more specialised, pollinator networks are still examples of diffuse coevolution (Russo et al., 2018), where specialised mutualisms are rare (Russo et al., 2016). Hence, alien species can become incorporated into local plant-pollinator networks (Emer et al., 2016), especially when they show similarities to native plants (Divíšek et al., 2018), with pollinators benefitting from the nectar of both alien and native species. For the plants, however, the interaction is not necessarily always beneficial, as due to morphological and behavioural constraints, nectarivorous animals may rob nectar from the flowers of alien plants without pollinating it (Ollerton et al., 2012). For example, in the case of *Nicotiana glauca,* in its native range the plant is pollinated by four hummingbird species and attracts a single nectar-robbing insect (Ollerton et al., 2012). However, in the plant's alien range, multiple species of birds and insects rob nectar from the plant (Ollerton et al., 2012). This is important to quantify as such species interactions limit the potential for alien plants to spread and become naturalised (Irwin and Brody, 1999).

The majority of existing work on interactions among pollinators and plants, including in urban areas, has been conducted in the northern hemisphere and in temperate areas (Baldock, 2020; Wenzel et al., 2020), which has focused largely on pollination by insects, especially bees (Millard et al., 2020). However, plants in tropical and subtropical regions depend on vertebrate pollinators heavily, with as much as 63 % of fruit or seed production lost when vertebrate pollinators are removed (Ratto et al., 2018). Cities in tropical and subtropical Africa and Asia are experiencing the fastest growth in the world. By 2030, more than half of the population on these continents will live in urban areas (Cohen, 2004). This creates challenges for human populations, including sufficient living space, waste management, and water availability (Yuen and Kumssa, 2011), with potential for massive consequences for wildlife that exceed those experienced in smaller urban agglomerations. Therefore, there is a need for innovative solutions to deal with the consequences for fauna and flora in megacities. These species have evolved under different environmental conditions to those predominantly explored in the rapidly growing field of urban ecology.

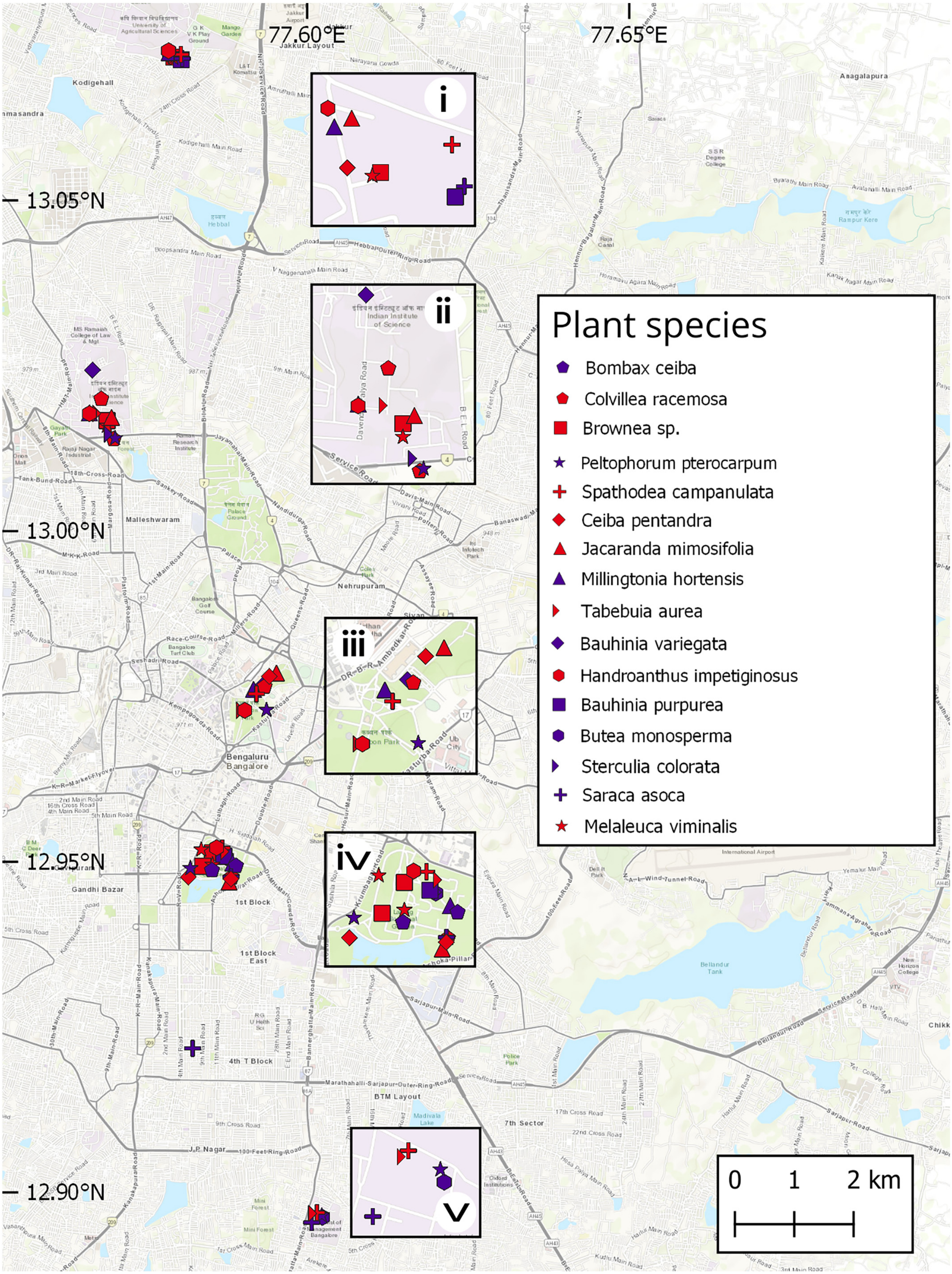
To address this knowledge gap, here we investigated whether native birds and mammals interact differently with native and alien plants in one of the world's most populous cities and largest urban areas, Bengaluru, India (United Nations, 2019). Due to its colonial past and extensive afforestation efforts undertaken in the 1980's (Neginhal, 2006), up to 77 % of the trees in the city's parks and avenues are of non-native origin (Nagendra and Gopal, 2010, 2011). However, the city has undergone rapid growth since the turn of the millennium, resulting in the loss of both planted and natural green cover (Sudhira et al., 2007). With the exception of irregular escapees from captivity, Bengaluru does not have any non-native bird or mammal species, making it an excellent case study, as interactions with alien plants are not influenced by competing alien pollinators. We first asked if occupancy by mammals and birds varied with the origin of trees (controlling for tree height and their floral display). Next, we compared species composition, richness and abundance of birds according to tree origin, before exploring whether avian and mammalian pollinators were more likely to engage in nectar theft (or flower depredation) on alien trees compared to native trees. For each question, we predicted native tree species to be preferred over alien tree species since they share a longer evolutionary and ecological history (Chrobock et al., 2013).

2. Methods

2.1. Study area

We focused on flowering tree species in Benguluru that are known to be pollinated by birds and diurnal mammals (Subramanya and Radhamani, 1993), and have been planted intentionally across the city. We classified trees that are native to regions outside of the Indian subcontinent as alien species using the Invasive Species Compendium (CABI, 2022), and then selected eight species each of native and alien trees (Electronic supplementary materials, Table S1). We identified up to four individuals of each tree species across different parts of the city (54 focal trees in total, Fig. 1) and wherever possible, we sampled two individuals in public areas and two in private areas to account for anthropogenic disturbances. The public areas consisted of large parks (Fig. 1 (iii) and (iv)), where a disturbance was in the form of people engaging in recreational activities like walking and running. The parks are of comparable size 300 and 240 acres respectively and have high footfall. Additionally, in (iii) on weekdays there is a public road open to traffic. The private areas consisted of educational campuses (Fig. 1 (i, ii and v)). The privates areas are of different sizes; i: 20 acres, ii: 440 acres and v: 100 acres. All the private campuses have some vehicular traffic moving through them, but this is curtailed to the people that have rights to visit the campus and hence not as much as public roads. They also have disturbances in the form of people walking through the campus, however this is

Fig. 1. Location of native (blue symbols) and alien (red symbols) trees ($N = 54$) sampled across Bengaluru, India. Tree species are listed in order of Fig. 2. Details of areas sampled are shown in inserts and included private campuses (i, ii, v) and public spaces (iii, iv). [Base map sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community]


77.60°E
77.65°E
13.05°N
13.00°N
12.95°N
12.90°N
i
ii
iii
iv
v
Plant species
Bombax ceiba
Colvillea racemosa
Brownea sp.
Peltophorum pterocarpum
Spathodea campanulata
Ceiba pentandra
Jacaranda mimosifolia
Millingtonia hortensis
Tabebuia aurea
Bauhinia variegata
Handroanthus impetiginosus
Bauhinia purpurea
Butea monosperma
Sterculia colorata
Saraca asoca
Melaleuca viminalis
0
1
2 km
Kodigehall
Jakkur Layout
Anagalapura
Hebbal
Malleshwaram
Nehrupuram
Bengaluru
Bangalore
Gandhi Bazar
1st Block
1st Block East
4th T Block
BTM Layout
7th Sector
Indian Institute of Science
Bellandur Tank
International Airport

once again less than the public areas. It was not possible to sample four trees for five of the native species (there are more alien than native tree species in Bengaluru (Nagendra and Gopal, 2010)), so for these we sampled as many individuals as possible (Electronic supplementary materials, Table S1).

2.2. Field methods

From December to March in 2019/20, we (PD and RS) observed each focal tree twice a month during a 30-min session where all visits by birds and mammals were recorded in 10-min intervals. One session per month was conducted between 7:00–10:00 am and the other between 15:30–17:30 pm to account for variation in activity levels of birds and mammals during the day. When there were no open flowers on a focal tree, the tree was observed for only ten minutes. No observations were carried out when it rained; however, there were few days with bad weather across the sampling period. Due to the COVID-19 pandemic, only a single observation session was conducted for each tree in March. Additionally, entry into one of the private areas was banned and hence six focal trees (of six different species) were not observed in March.

All trees had sufficient space around their canopies to allow observations (using binoculars) of any birds entering the tree against the sky. Even if the bird entered the tree on the far side from the observer, we do not expect visibility to differ between native and alien trees as the focal trees were of a similar height on average. This was also the case with mammals as they were conspicuous while moving in the trees. When there were multiple animals in the focal tree, those interacting with inflorescences were observed preferentially. If there were multiple animals interacting with inflorescences at the same time the animal which was sighted first was observed till it moved away from the inflorescence and then the next animal was observed. At any given time during the focal observations, there were no more than three or four animals interacting simultaneously with inflorescences. All interactions of birds and mammals with an inflorescence were classified as follows: (a) Potential pollination (hereafter, ‘pollination’): animal observed to insert head/tongue into the flower; (b) Nectar robbing: animal making an incision in the flower, hence taking nectar without touching anthers; (c) Flower depredation: animal consuming a flower or bud, in whole or part, from the tree.

Floral display size is known to affect the rate of visitation by pollinators (Schmid-Hempel and Speiser, 1988) therefore we estimated the number of open flowers on the focal trees as follows: we counted the number of open flowers on five inflorescences using binoculars and then multiplied the average number of flowers within an inflorescence with the total number of inflorescences on the tree. Additionally, as larger trees may hold a larger number of animals, we estimated the size of the tree by measuring its height using the Smart Measure app (Boy, 2010). Briefly, the app measures the distance between the observer and the object at its lowest and highest points to calculate its height.

2.3. Statistical analysis

All analyses were carried out in R (version 3.6.1) (R Core Team, 2019). First, we investigated whether birds and mammals occupy native trees more than alien trees. Each 10-min interval of a focal observation session was given a value of 1 if a bird or mammal (based on Indian palm squirrel, *Funambulus palmarum,* data only; single bonnet macaque, *Macaca radiata*, observation removed) of any species was seen in the tree and 0 if they were not. The occupancy values were summed for every 30-min session. In the case when a tree did not have any open flowers the session was only 10 min long and had a maximum value of 1 for occupancy or absence of animal. These were then used in a GLMM as a bound response variable (using the cbind function) and a binomial error distribution to avoid a three-way nested random effect. In both models for birds and mammals, the effect of tree origin (native or alien) was tested by including it as an independent variable in separate two-way interactions with floral display size (transformed using natural logarithm plus one to account for the vast variation in floral display sizes) and tree height. Tree origin, height, and floral display size were not significantly correlated ($r_{\text{floral display size, height}} = -0.05$, $r_{\text{floral display size, origin}} = -0.18$, $r_{\text{Origin, height}} = -0.16$). To account for repeated observations of individual trees, tree ID was included as a nested random effect within tree species. The date of observation was also included as a random effect to account for variation in weather between sampling days as this was not expected to vary linearly.

Second, we examined whether bird species composition, richness and overall abundance varied with the origin, floral display size and the height of the trees. This part of the analysis did not include mammals as we only observed two species. For species composition, we made a matrix of the number of individuals of each species occupying the 54 focal trees and then tested whether the dissimilarity indices differed according to tree origin in interaction with the average number of flowers and tree height using a permutational multivariate analysis of variance (PERMANOVA). Species composition (i.e. relative species abundance) was visualized using a non-metric multidimensional scaling (NMDS) ordination plot. Both the PERMANOVA and NMDS plot were produced using the ‘vegan’ package (Oksanen et al., 2019). We calculated species richness (i.e. number of species present) and overall abundance (i.e. number of individuals present) for each 30-min focal session. This was tested against the tree origin with separate two-way interactions with floral display size (transformed using natural logarithm plus one to account for the vast variation in floral display sizes) and tree height, using GLMMs with poisson error distribution. As in the occupancy models, tree ID nested within tree species and the date of observation were added as random effects.

Finally, we examined the outcomes of fauna interacting with inflorescences of native versus alien trees. For birds, pollination-type behavior was counted as a ‘success’ and nectar-robbing as a ‘failure’ and summed across all observations per session where either interaction occurred (no successes were entered as 0). These were then used in a GLMM as a bound response variable (using the cbind function) and a binomial error distribution. As there was only a small number of observation sessions ($N = 43$) we did not include two-way interactions, and tree origin was included as a response variable with separate models for the additive effect of log of floral display size or tree height. Tree ID nested within species was added as a random effect to account for repeated observations of trees. All interactions of birds with *Melaleuca viminalis* were excluded from this analysis as it was not possible for the birds to cheat due to the floral structure of this plant. For mammals, we used a Fisher's exact test to explore if pollination or depredation was more likely for alien tree species as we did not observe any instances of pollination of native species.

All GLMMs were implemented using the ‘lme4’ package (Bates et al., 2015), and the adequacy of the maximal model's fit to the data were checked using the DHARMa package (Hartig, 2021) which visualizes and provides statistical tests of normality and heterogeneity of model residuals. Within each analysis, the maximal model was compared using its AICc score (AICcmodavg package; Mazerolle, 2020) to a null model, and models containing only tree origin or including one or more of its interactions or other independent variables where appropriate. The model with the lowest AICc (ΔAICc >2) was selected as the model of best fit (Burnham and Anderson, 2004). When there were multiple competing models, we disregarded models with uninformative predictors other than tree origin, our key variable of interest (Arnold, 2010). Full results from each set of models are provided in the supplementary materials as indicated below.

3. Results

From a total of 125 h and 40 min of observations (350 sessions divided into 754, 10-min intervals), we detected 32 species of birds (Fig. 2) and 2 species of mammals (Indian palm squirrel, 156 intervals; bonnet macaque1 interval) present in the 16 species of trees (54 focal trees, Fig. 1). More trees were occupied by birds in public areas than private areas ($\chi^2 = 8.309$, $p = 0.003$), this difference was not observed when birds were interacting with flowers ($\chi^2 = 0.001$, $p = 0.970$). The behavior of animals on the trees varied from being present (birds = 54.7 % of the intervals, mammals = 20.8 % of intervals) to interacting with flowers in a manner that could

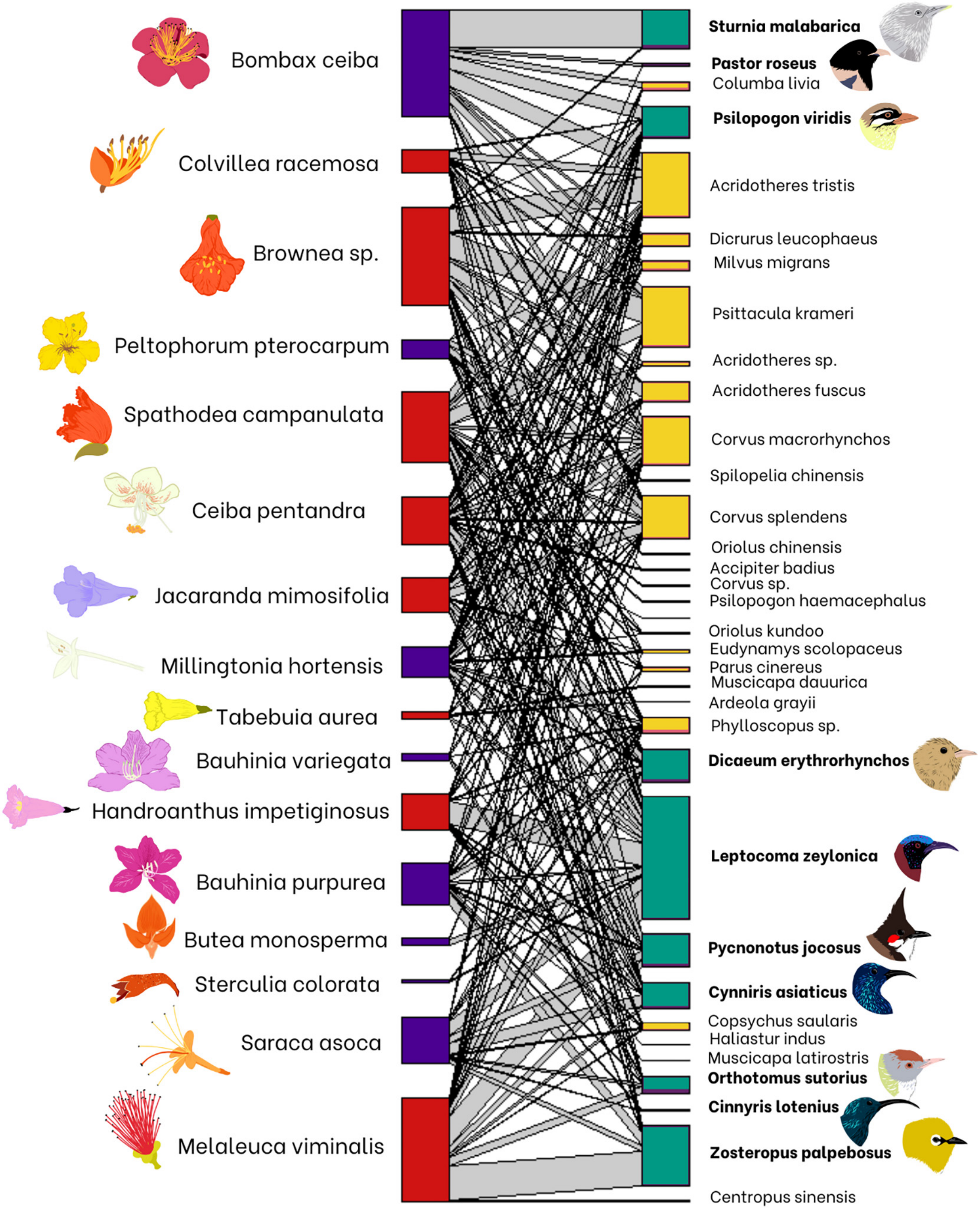


Fig. 2. Interaction web of bird species ($N = 32$) observed using native (blue bars, $N = 8$) and alien (red bars, $\mathrm{N} = 8$) urban tree species. Bird species interacting with the inflorescences of the trees are indicated in green with bold font and with a picture of the bird next to the species name. Bird species occupying a tree without interacting with the inflorescence are shown in orange. Bar height shows the relative number of times a species was observed. The width of connecting lines indicates the number of interactions between two species.

have facilitated pollination (birds = 126 times; mammals = 32 times), nectar theft (birds only, 85 times) or predation (i.e. eating flowers; mammals only, 47 times). Both species of mammals were observed interacting with inflorescences but only 10 of the 32 species of birds interacted with inflorescences (Fig. 2).

3.1. Factors affecting occupancy of trees by birds and mammals

For both mammals and birds, models with the lowest ranked AICc scores (< 2 AICc from the next model) contained the interaction between tree origin and height (Electronic supplementary materials, Table S2). The occupancy of trees by birds differed according to tree origin (details of model with lowest AICc: Electronic supplementary materials, Table S2), and this depended on tree height (height*origin, $z = -2.279$, $p = 0.022$, Fig. 3a; Electronic supplementary materials, Table S3a). Among trees taller than 12–18 m (i.e. from crossing point of slopes to where 95 % confidence intervals diverged), birds tended to be more likely to occupy alien species (Fig. 3a). Occupancy for birds increased with overall size of the floral display ($z = 6.294$, $p < 0.001$), but this did not vary according to tree origin (Electronic supplementary materials, Table S3a). In the case of mammals, there was a similar trend indicating that occupancy of trees varied with origin and tree height, but this was approaching statistical significance (height*origin, $z = -1.823$, $p = 0.068$; Fig. 3b; Electronic supplementary materials, Table S3b). When the data were reanalyzed

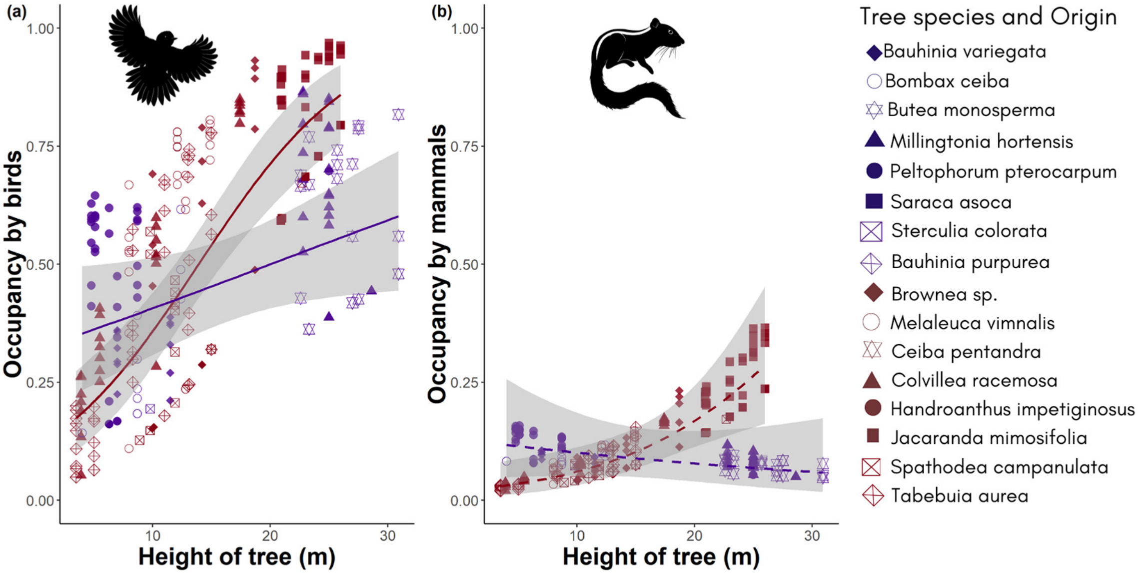


Fig. 3. Probability of alien and native trees being occupied by (a) birds and (b) mammals. Lines (with 95 % confidence intervals shown as grey bands) and data points represent model predictions for occupancy of native (blue) and alien (red) trees at different heights. Solid lines indicate statistically significant results. Taller alien trees are more likely to be occupied by birds.

without the interaction effect, tree origin (our main variable of interest) was not a significant predictor of tree occupancy by mammals (origin, $z = -0.153$, $p = 0.878$; Electronic supplementary materials, Table S3c).

3.2. Factors affecting bird species composition, species richness, and abundance

As well as occupancy, taller alien trees also supported a greater relative diversity of bird species than native trees of a similar height ($r^2 = 0.048$, $F_{(1,54)} = 2.986$, $p = 0.007$; Fig. 4). Floral display size also explained 7 % of the variation in species composition (Electronic supplementary materials, Table S4). Tree origin was present in the models with the lowest AICc scores for bird abundance and species richness. In the case of species richness, there is a trend approaching statistical significance that native trees are less species rich ($z = -1.804$, $p = 0.071$; Electronic supplementary materials: Table S5). However, native trees with larger floral display sizes were seen to be more species rich than alien trees with large floral displays ($z = 2.322$, $p = 0.020$; Electronic supplementary materials: Table S5). Finally, species richness also increased with tree height ($z = 3.546$, $p = 0.003$; Electronic supplementary materials: Table S5) However, bird abundances did not differ significantly according to tree origin, although abundances increased with tree height, this trend was not statistically significant (Electronic supplementary materials, Table S6).

3.3. Pollination or nectar theft and flower depredation in native and alien trees

Finally, the types of interactions that occurred between birds and mammals with flowers also tended to differ according to tree origin (Fig. 5). Pollination-type behavior tended to occur more often than nectar theft when birds visited native trees (Fig. 5a), yet while the model with the lowest AICc score included tree origin (Electronic supplementary material: Table S8), this trend was not statistically significant ($z = 1.369$, $p = 0.171$; Electronic supplementary materials: Tables S7). Closer inspection of the data, however, showed that there was only variation in behavior among alien focal tree species (Electronic supplementary materials: Fig. S1). When we repeated our analyses without tree species as a random effect in the model, the trend for birds to be more likely to pollinate native trees was statistically significant ($z = 2.270$, $p = 0.023$; Electronic supplementary materials: Table S8). In the case of diurnal mammals, both pollination and depredation occurred in alien trees, but native trees were less likely to be pollinated than alien trees (Fisher's exact test, $p = 0.002$; Fig. 5b).

4. Discussion

With rapid increases in urbanization (Yuen and Kumssa, 2011), and concomitant issues of biotic homogenization and loss of resources (McKinney, 2006), there is a pressing need to improve our understanding of interactions between native and alien flora and fauna. This is particularly important, as previous assumptions that alien species always have negative impacts on ecosystems are currently being challenged (Davis et al., 2011). Here we explored these relationships to provide one of the first examples from a tropical megacity: Bengaluru. We found that native birds and mammals use both alien and native trees, but the diversity of bird communities tends to be greater in alien than native trees of the same height. Species richness of birds increased with tree height, additionally, native trees with large floral displays had more species than alien trees with similarly sized floral displays. Furthermore, we found that avian pollinators were more likely to cheat while interacting with alien species but mammals were more likely to depredate the flowers of native species. However, we only observed two species of mammals: Indian palm squirrel (*Funambulus palmarum*) and bonnet macaque (*Macaca radiata*), with the bonnet macaques only observed once, so the differences in interactions we detected are limited to squirrels. Overall, our results suggest that the availability of native and alien trees may influence faunal diversity in this megacity, and that differences in how birds and mammals use floral resources are likely to have consequences for the invasion potential of alien trees.

Whether pollinators prefer to pollinate alien or native species varies from case to case (natives pollinating natives, e.g. (Buchholz and Kowarik, 2019; Fukase and Simons, 2016; Pardee and Philpott, 2014); natives pollinating aliens, e.g. (Pyšek et al., 2011)) and studies are only beginning to explore these interactions in an urban context. As would be expected due to shared evolutionary histories, we found an indication that avian pollinators were more likely to behave in a way that could lead to pollination in native trees. While in native trees, birds consistently engaged in pollination or nectar theft, in alien species there was more variation in behavior. Most of the alien trees in our study system had tubular flowers, and we saw that avian pollinators engaged in nectar theft similar to other studies (Irwin and Maloof, 2002). However, the tubular shape of the flowers is likely not the only reason to explain nectar theft behavior as the birds were also seen to pollinate the flowers of the same alien species occasionally and also pollinate tubular native flowers. Nectar theft from alien species could harm their seed set and hence reduce their invasion potential (Irwin and Brody, 1999; Roubik,

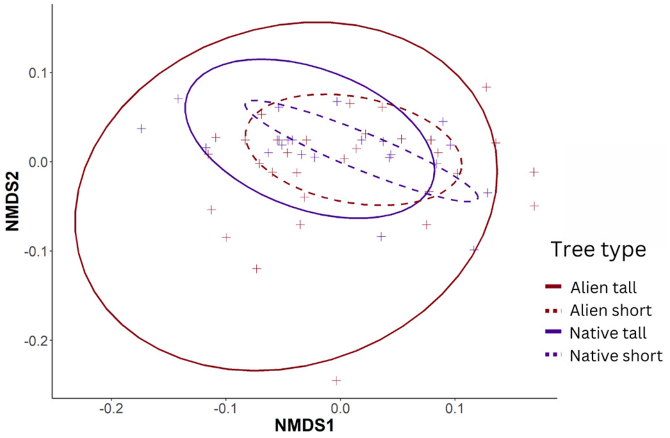


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot of the species composition of birds occupying alien and native trees that were either shorter (alien in red, native in blue) or taller (in solids lines) than the mean heights within group of origin using the Gower index. Crosses indicate dissimilarity values for the species composition of each focal tree ($N = 54$), crosses that are closer to each other are trees with similar species composition and ellipsoids are superimposed normal-probability contours over a scatterplot to aid visualization and interpretation. Alien species support the most diverse community of birds when the trees are tall.

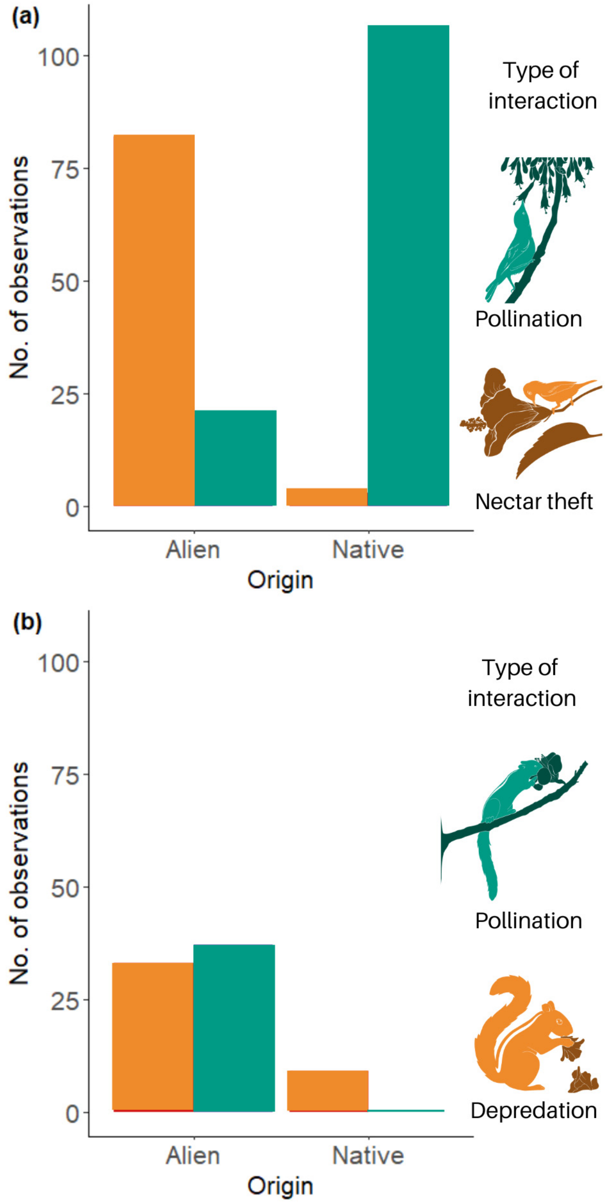


Fig. 5. Different interactions with inflorescences displayed by (a) birds and (b) mammals. Pollination attempts are shown in green. Nectar theft and flower depredation are shown in orange. The icons are indicative of each taxonomic group and for mammals, all but one observation were of squirrels. No pollination interactions were observed by mammals on native trees.

1982). Additionally, our sample size of trees where interactions were observed was small. We observed as many different tree species as possible and as many individuals as was feasible given the constraints of our study site, and it would be difficult to include many more additional tree species as we were limited due to past planting decisions made in the city. Nevertheless, expanding our study to other tropical megacities in India and abroad would help to test the generality of our findings. Additionally, we found that mammals (mostly squirrels) were more likely to pollinate alien species. This may be because the alien trees in our study were largely from South America, and are thought to have evolved floral traits to support pollination by non-flying mammals (Carthew and Goldingay, 1997). Surprisingly, we never observed either squirrels or macaques pollinating native species but instead they consumed the flowers. Both are omnivores (Menon, 2009) and could be making use of flowering trees for food in the absence of fruiting trees in the city. Despite this, it is unlikely that the pollination interactions by squirrels would compensate for the nectar theft by birds, as squirrels also depredated all the species they were seen to pollinate.

Previous work has shown that, globally, fauna are more likely to have positive interactions with alien woody species than grasses and weeds (Kuebbing and Nunez, 2015). Here we also found a trend that, apart from interactions like pollination, which may require specialised physiological and morphological adaptations, behaviours like perching, roosting, nesting etc. (and hence occupancy, species diversity and bird species composition) tended to increase with an increase in tree height. This was an intuitive result as larger trees allow more space for birds and could help birds avoid anthropogenic disturbances (Suhonen et al., 2017). However, in the case of birds, beyond 12–18 m, alien trees were occupied preferentially compared to native species. This along with our results of birds robbing nectar from the alien species could indicate that the alien species have poor invasion potential, while at the same time providing an important refuge in a greying city. It is unclear why taller alien trees were preferred and this pattern warrants further investigation. A similar pattern is seen for bird species richness which is higher in native trees with larger floral display size than alien trees with similar floral display sizes. This pattern also cannot be explained by our methods and warrants further investigation to understand the various trophic interactions that might be taking place.

Cities are known to be gateway nodes through which introduced species can begin to spread (Francis and Chadwick, 2020). However, in megacities there are large regions covered in impervious surfaces, which do not allow establishment of seedlings and could potentially hinder the spread of alien species more than in smaller urban agglomerations. For example, in Bengaluru an estimated 60 % of area in the municipality limits is covered by impervious surfaces and only 14 % area where seeds can potentially take root (*Personal comms, Dr. Sudhira HS., BBMP land cover based on ESA 2020*). Additionally, other plant traits like mode of dispersal are important to understand if a tree species could be a harmful invasive (Hejda et al., 2009). Data on plant traits along with interactions of seed dispersers and pollinators can help us make informed decisions about what and where alien species can be planted in a megacity such that there is reduced risk of invasion, while still allowing positive interactions with the city's fauna. Another policy perspective from our study is that animals prefer taller trees. Nagendra and Gopal (2010) have shown that on narrower roads in Bengaluru, planting decisions favour shorter tree species with narrow canopies (Nagendra and

Gopal, 2010). Interactions with native species can be encouraged by allowing native species to grow taller, rather than cutting down alien species. This trend of planting shorter "more manageable" trees is unlikely to be specific to Bengaluru and can affect biodiversity in cities around the world. Greater canopy cover irrespective of the origin of tree species ensures that cities are cooler (Schwaab et al., 2021), this could be especially important as due to impervious surfaces cities are experiencing record breaking heat waves each year (Ziter et al., 2019). Additionally, in other parts of the world, alien species are introduced on purpose to keep up with climatic changes brought on by anthropogenic climate change (Alizadeh and Hitchmough, 2018). In such a scenario too, exploring interactions of the local fauna with the introduced flora is of the utmost importance to maintain healthy ecosystems.

As in many urban areas, mature trees planted extensively across Bengaluru are now at threat of felling due to both development and concerns over their alien origin. However, our results highlight the importance of avian pollinators to native trees in urban spaces and the importance of alien trees to the urban faunal community. To better estimate the invasion potential of alien trees, however, it is necessary to expand our knowledge to include other potential pollinators not encountered during our study and which pollinate species of trees which are not included here. For example, many species of bats in the region are endangered (Kumar and Kanaujia, 2009) and understanding their nocturnal interactions with urban tree resources might also help in making the city more hospitable to them. We were also unable to quantify visits by invertebrate pollinators, or the contributions of invertebrates and vertebrates to seed set. This is especially important since invasive insect species are known to exist in the region (El-Shafie, 2020) and these could aid the pollination of alien trees further, as alien insects are known to preferentially interact with alien flora (Hanley and Goulson, 2003). However, the flowers of eight of the sampled species showed typical ornithophilous features, suggesting that the effects of invertebrates compared to avian pollinators may be limited in these cases.

5. Conclusion

In summary, our results indicate that both alien and native trees in the city provide important resources to birds and mammals, with limited potential for invasion. Interactions of birds varied with not only the origin of the tree but also the tree species. This suggests that policy informaing urban plantation drives need to take into account a case-by-case understanding of which plant species can support fauna in the city while reducing the potential for spread of invasive species.

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CRediT authorship contribution statement

PD conceived the ideas and designed methodology with guidance from RT and AL; PD and RS collected the data; PD analysed the data with guidance from RT and AL; PD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The data and code used for this article are available in an open online repository at https://doi.org/10.5281/zenodo.7445861

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.

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Appendix A. Supplementary data

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