Sacred fig trees promote frugivore visitation and tree seedling abundance in South India

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While sacred groves (forest fragments protected for religious reasons) are widely acknowledged to have a beneficial effect on biodiversity conservation, the ecological benefits of individual sacred trees remain unknown. Fig trees are present as sacred trees in human-dominated landscapes across South Asia and are considered keystone species for wildlife in tropical forests. If frugivores continue to visit fig trees in disturbed landscapes, they may deposit seeds of other tree species beneath fig canopies, ultimately facilitating forest regeneration. We studied whether sacred fig trees in Tamil Nadu, India can facilitate seed dispersal in human-dominated landscapes. We quantified abundance of sacred fig trees at the study site, assessed whether seed-dispersing frugivore visitation to fig trees is affected by human disturbance, and compared tree seedling density beneath fig trees and open areas. We found that some species of frugivorous birds and bats will visit large fig trees in conditions of high human disturbance and that tree seedling density is significantly higher under sacred trees compared to open areas. By promoting frugivore activity, sacred fig trees may have a beneficial effect on biodiversity conservation in human-dominated landscapes.

Keywords: *Ficus* sp., frugivory, human disturbance, *Pteropus* sp., seed dispersal, urban ecology.

INTEGRATING traditional knowledge with natural resource management can benefit biodiversity conservation. For example, sacred groves, forest fragments where there are religious taboos against cutting trees and hunting wildlife, are widely acknowledged to have a beneficial effect on conserving biodiversity and maintaining ecosystem services[1]. Several studies have demonstrated higher plant biodiversity in these forest fragments than in formal reserves[1,2]. The same cultural traditions that have protected sacred groves have also preserved individual trees in human-dominated landscapes[3]. However, whether or not sacred trees can facilitate natural ecosystem processes in human environments remains unknown.

Fig trees (genus *Ficus*) are considered sacred in India[4], East Asia and Africa[5] and are common in agricultural and urban landscapes where other large trees are absent. In natural forests, fig trees may be keystone species, providing food for wildlife when other resources are scarce, and supporting a high density and diversity of frugivores (fruit-eating animals)[6,7]. If frugivorous birds and bats continue to visit fig trees located in sites with high human disturbance, sacred fig trees may promote frugivore abundance. One beneficial consequence of frugivore visitation to isolated fig trees in human landscapes could be the dispersal of seeds of other tree species into the soil beneath fig canopies, where a favourable microclimate may promote survival and growth of woody plants[8–10]. If the density and diversity of woody seedlings is higher under fig tree canopies compared to open microsites, sacred fig trees may have the potential to increase woody vegetation cover in disturbed areas.

We assessed whether sacred fig trees promote animal seed dispersal in a human-dominated landscape in Tamil Nadu, India. First, we measured the abundance of sacred fig trees in the landscape. Next, we quantified the effect of human disturbance on bird and bat visitation to isolated fig trees. Finally, we compared woody seedling density beneath fig tree canopies, a non-fig tree species and open riparian and degraded sites. Because sacred fig trees are a common feature of agricultural and urban landscapes across South Asia, their role in seed dispersal, a critical ecosystem process, has broad implications for biodiversity conservation in the region.

The study was conducted in Tirunelveli District, Tamil Nadu, South India (8°40.426′N, 77°26.642′E). The area is a matrix of agricultural land, small villages, overgrazed pasture and disturbed tropical dry deciduous forest on the border of the Kalakad–Mundanthurai Tiger Reserve. The human density at the site is approximately 150 people/sq. km. At this site we surveyed a circular area of ~50 sq. km for large (>60 cm DBH; diameter at breast height) fig trees and visually assessed whether each fig tree was associated with a religious structure, such as a temple or a shrine.

We recorded visitation rates to *Ficus benghalensis* trees, the most common sacred fig tree in the study site, for nine bird species and one species of fruit bat, *Pteropus giganteus*, the Indian flying fox. The bird species studied include house crow (*Corvus splendens*), Asian koel (*Eudynamys scolopacea*), red-vented bulbul (*Pycnonotus cafer*), and common mynah (*Acridotheres tristis*). Pteropodid bats and these bird species represent some of the primary dispersal agents for trees in the disturbed South Asian ecosystems[11].

During May–July 2006, we observed frugivore activity at 22 randomly selected *F. benghalensis* trees, all near peak fruiting period with DBH > 50 cm. Each tree was observed once to record bird and bat visitation. Focal tree locations ranged from areas of high human and vehicular

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Table 1. Comparison of seven models for predicting *Pteropus giganteus* visitation to focal trees

Model	K	ΔAIC_c	w_{ic}
DBH of focal tree	3	0.00	0.62
DBH of focal tree + building cover	4	3.15	0.13
Building cover	3	3.74	0.10
Neighbouring trees	3	3.76	0.09
Neighbouring trees + building cover	4	5.78	0.03
DBH of focal tree + building cover + neighbouring trees	5	6.63	0.02
DBH of focal tree + neighbouring trees	4	451.55	0.00

K is the number of parameters in the model (including the Y-intercept), AIC_c is the Akaike information criterion for small sample sizes, ΔAIC_c is the difference in AIC for small sample sizes between the best model and the current model, w_{ic} are the Akaike weights and DBH is the diameter at breast height.

traffic within villages, to groves of trees on the boundary of the Kalakad–Mundanthurai Tiger Reserve, up to 2 km away from human settlement. As an indicator of tree size, we measured DBH for each tree observed, treating aerial roots as individual stems. We measured two indicators of human disturbance within a 30 m radius around focal trees: neighbourhood tree cover, the sum of DBH of all trees >30 cm DBH, and building cover, a visual assessment of the area occupied by buildings on a scale of 1–5, where 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80% and 5 = 81–100% of the area within the neighbourhood covered by buildings. Previous research on frugivore feeding tree preferences has shown a significant effect of plant neighbourhood at this scale[12].

The number and species of birds in *F. benghalensis* trees were recorded from 0700 to 1000 h, the peak foraging period for frugivorous birds in the area (Caughlin, pers. obs.). To quantify bird visitation we used a scan sampling technique, recording the number of individuals and species identity of each bird in the tree every 15 min during the observation period. The average number of birds detected during scans for each focal tree during the 3 h period of observation was used for analysis of bird visitation. Bat observations took place from 1900 to 2200 h, which spanned the peak visitation period (2000–2100 h) reported in a study of *P. giganteus* foraging from the same region[13]. The total number of bat entries per tree was used to provide a single number for analysis of bat visitation.

We used generalized linear models, with bird and bat visitation as response variables with an underlying normal and negative binomial distribution (respectively) and log(DBH) of focal fig trees, neighbourhood tree cover and building cover as predictor variables. We checked for correlations between our predictor variables using Pearson's correlation diagnostic and found no correlations greater than 0.30. The main objective of the analysis was to compare the relative importance of neighbourhood tree cover, building cover and tree size for frugivore visitation. We constructed seven models with various combinations of predictor variables for each species (Table 1) and compared models using the altered small-sample version the Akaike information Criterion (AIC_c), representing the relative goodness of fit of each model[14,15]. We ranked the

predictive ability of models using AIC_c and determined the relative importance of each predictor variable using the sum of the Akaike weights, which can be interpreted as the probability that the current model is the best fit to the data. Finally, we calculated the parameter estimates and standard error for the variables weighted across all models.

In May–July 2006, we measured seedling density beneath individuals of two tree species, *F. benghalensis* and *Madhuca longifolia* (Sapotaceae), and treeless open riparian and degraded areas. While some *Ficus* individuals were fruiting during this period, *Madhuca* individuals were not. Species were collected, preserved and identified by a plant taxonomist at a nearby biological field station. *Madhuca* trees were selected for comparison to *Ficus*, because while *Madhuca* trees are also considered sacred in the study region and present in the same habitats as *Ficus*, *Madhuca* trees differ from *Ficus* trees in several key traits. *Madhuca* fruits have large seeds and attract a smaller assemblage of bird and bat species than fig trees, and *Madhuca* seeds can germinate beneath the canopy of the parent tree, unlike *F. benghalensis* seeds which are hemiepiphytes and tend to germinate in tree canopies or rocky crevices. Trees and open sites were randomly selected, with 10 replicates for each microsite. At each replicate, we recorded the number and species of every tree or shrub seedling in randomly placed 10 m² quadrats. Seedlings were defined as woody plants < 1 cm diameter at the midpoint of the stem. We only counted naturally dispersed seedlings, excluding those potentially planted by people. Riparian sites were located within 10 m of the banks of the Tambirapani River and open degraded sites were located in any open area not adjacent to the river or a tree canopy. All sampling sites were located at least 100 m apart and we excluded areas where the ground had been recently cleared by people. In order to test for the effects of isolated trees on woody seedling density, we used one-way ANOVA with seedling density as the response variable, and treatment category as the predictor variable.

A total of 244 *F. benghalensis*, 108 *Ficus religiosa* and 15 *Ficus infectora* trees were found in the area, with a total density of 0.0734 figs/hectare. 61.4% of *F. benghalensis*, 95.3% of *F. infectoria* and 100% of *F. religiosa*

were associated with temples. A typical sacred *F. benghalensis* tree next to a roadside temple is shown in Figure 1.

Twenty-two *F. benghalensis* trees were observed for frugivore activity for a total of 120 h. Eleven frugivorous animal species were observed feeding on trees. The mean number of birds visiting a tree during each 3 h observation period was 11.98, with a standard deviation (SD) of 11.59. Common mynahs accounted for 72.3% of bird visitation to fig trees, followed by house crows (15.5%), Asian koels (6.2%) and red-vented bulbuls (3.6%). All these bird species were frequently seen eating figs. Three other bird species and unidentified birds made up the remaining 2.6% of visitations. The mean number of flying foxes observed visiting fig trees per 3 h observation period was 29.35, with a SD of 41.40.

The best model for predicting bat visitation consisted solely of the DBH of the focal tree (Table 1). Support for more complex models was limited as the next best-fitting model, including DBH and building cover had a ΔAIC_c of 3.15. The summation of the Akaike weights (Σw_{ic}) for individual variables demonstrated that the size of the focal tree was the most important variable predicting bat visitation ($\Sigma w_{ic} = 0.77$), followed by building cover ($\Sigma w_{ic} = 0.28$) and neighbouring trees ($\Sigma w_{ic} = 0.14$). Bat visitation was positively correlated with DBH of the focal tree (Figure 2).

The best models predicting bird visitation included DBH of the focal tree and the summed DBH of neighbouring trees (Table 2). The best model incorporated both the size of the focal tree and the DBH of the surrounding trees, whereas the second best model ($\Delta AIC_c = 2.40$) incorporated only DBH of the focal tree. All other models had $\Delta AIC_c > 3$. The summation of the Akaike weights between models for different variables predicting bird visitation revealed DBH of the focal tree to be the best predictor of bird visitation ($\Sigma w_{ic} = 0.99$),

followed by summed DBH of neighbouring trees ($\Sigma w_{ic} = 0.76$), and building cover ($\Sigma w_{ic} = 0.16$). We found a positive correlation between focal tree DBH and bird visitation (Figure 3) and a negative correlation between bird visitation and neighbourhood tree cover.

A total of 294 woody seedlings from ten different tree species were recorded, with 283 seedlings located under tree canopies and 11 located in riparian or degraded areas (Table 3). Ten of these seedling species were animal-dispersed and one was wind-dispersed. Four species were naturally occurring forest species in the bioregion, whereas nine seedling species were associated with humans in the area, commonly planted in public spaces
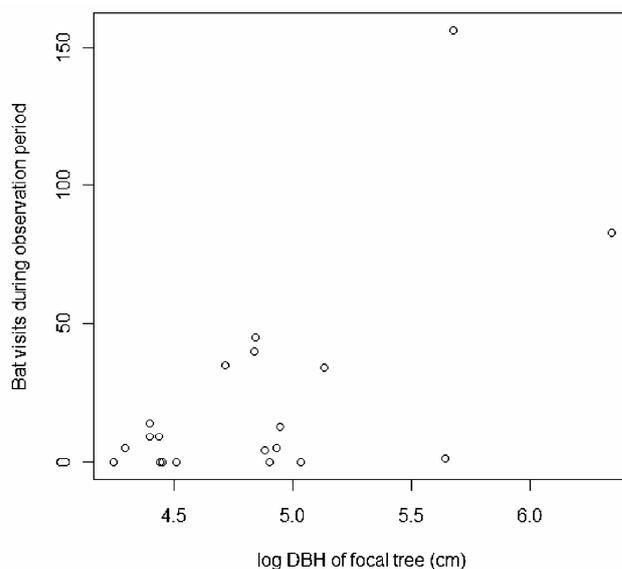

Figure 2. *Pteropus giganteus* visitation to fig trees as a function of log-transformed diameter at breast height (DBH; in cm).
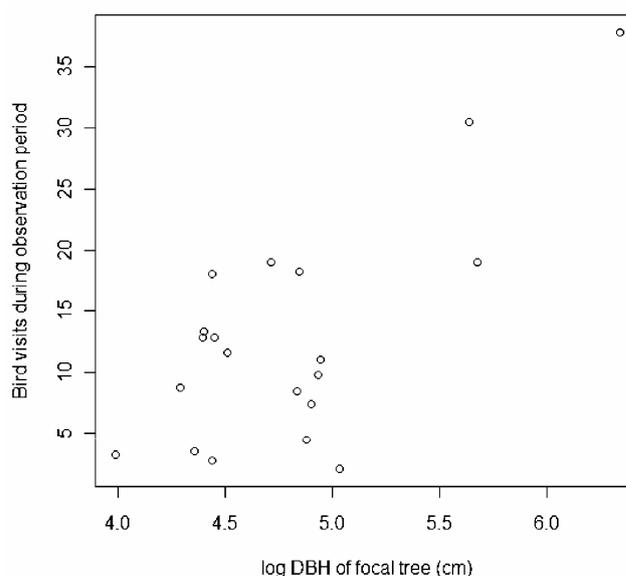

Figure 1. A typical *Ficus benghalensis* tree located next to a temple at the study site. Photo credit: A. Saravanan.

Figure 3. Bird visitation to fig trees as a function of focal tree log-transformed DBH (in cm).

Table 2. Comparison of seven models predicting bird visitation to focal trees

Model	K	ΔAIC_c	w_{ic}
DBH of focal tree + neighbouring trees	4	0.00	0.64
DBH of focal tree	3	2.40	0.19
DBH of focal tree + building cover + neighbouring trees	5	3.40	0.12
DBH of focal tree + building cover	4	5.36	0.04
Neighbouring trees	3	16.24	0.00
Building cover + neighbouring trees	4	19.40	0.00
Building cover	3	20.65	0.00

Table 3. Tree and shrub seedlings found in the study

Species	F	M	R	D	Total	Source	Dispersal
Morinda citrifolia L. (Rubiaceae)	46	44	5	2	97	N, H	Animal
Azadirachta indica L. (Meliaceae)	41	18	4	0	63	N, H	Animal
Madhuca longifolia (L.) J.F. Macbr. (Sapotaceae)	0	44	0	0	44	H	Animal
Murraya koenigii (L.) Sprengel (Rutaceae)	7	9	0	0	16	H	Animal
Streblus sp. (Moraceae)	3	5	0	0	8	N	Animal
*Thevetia neriifolia** L. (Apocynaceae)	14	0	0	0	14	H	Wind
Polyalthia longifolia Sonn. (Annonaceae)	3	0	0	0	3	H	Animal
Ficus religiosa L. (Moraceae)	0	3	0	0	3	H	Animal
Citrus sp.* (Rutaceae)	2	0	0	0	2	H	Animal
Syzygium cuminii (L.) Skeels. (Myrtaceae)	2	0	0	0	2	N, H	Animal
Meliaceae*	0	42	0	0	42	–	Animal
Total seedling abundance	118	165	9	2	294		
Total seedling species richness	8	7	2	1	11		

*Indicates the seedling species was found only beneath a single isolated focal tree.
N, Naturally occurring; H, Cultivated by humans; F, Ficus; M, Madhuca; R, Riparian; D, Degraded.

and gardens. The highest number of seedlings per individual site occurred under *Madhuca* trees, with a mean and SD of 16.5 ± 9.0 seedlings. A lower number of seedlings occurred beneath *Ficus*, with a mean and SD of 11.7 ± 6.1. In contrast to both treatments with tree species, open degraded and riparian sites had very low seedling density with comparatively little variation (degraded: 0.2 ± 0.4 seedlings, riparian: 0.9 ± 1.3 seedlings). One-way ANOVA demonstrated significant effect of treatment on seedling density (F-ratio = 6.53, $P < 0.001$).

Our results suggest that sacred fig trees in South India are likely to promote animal seed dispersal and tree seedling recruitment in human-dominated landscapes. In a survey of 367 large (DBH > 60 cm) *Ficus* trees at the study site, 73% of the trees were associated with temples and shrines, indicating that religion is a critical driver of fig tree conservation in India. Tree size was more important than the effects of human disturbance in explaining visitation by Indian flying foxes and frugivorous birds, suggesting that these animals will continue to visit large trees even in urban areas. Finally, the area beneath large isolated trees contained a significantly higher abundance of animal-dispersed tree seedlings compared to open areas. Consequently, isolated fig trees in the landscape could become focal points for expansion of woody vegetation. Recognizing the value of sacred fig trees as a food resource for frugivorous animals and a recruitment site for woody seedlings could lead to improved biodiversity conservation in human-dominated landscapes.

In this study, birds and flying foxes continued to visit large *F. benghalensis* trees in areas of high human disturbance. Other tree species may fail to attract frugivores in sites with high human activity[16] and the ability of figs to attract a wide range of frugivores may contribute to their usefulness for biodiversity conservation[8,11]. The large number of bats observed visiting trees in areas with high building cover and associated human presence is especially surprising considering that flying foxes are hunted in the area. Bats may have visited human-inhabited areas regardless of potential risks because of greater food sources available in yards, orchards and near temples, relative to the uninhabited areas. Despite the relative unimportance of human disturbance for bat foraging, bat activity may be negatively influenced by humans in other ways, for example, disturbance of roost sites[17]. The 10 different bird species observed eating figs were largely those well-adapted to human settlement, representing only a fraction of the diverse assemblages of fruit-eating birds observed feeding on the fruit of fig trees in undisturbed forests of the area[18]. While neither *P. giganteus* nor the bird species we observed are considered threatened, increased abundance of these animal species in the landscape could promote seed dispersal, leading to increased tree recruitment.

Similar to previous studies elsewhere in the world[8,10], we found significantly higher seedling density beneath isolated trees compared to open areas, with 96.9% ($n = 294$) of seedlings occurring beneath *Ficus* and

Madhuca trees. Because we did not quantify patterns of seed rain in this study, it remains unclear whether higher seedling density and diversity beneath focal trees was a consequence of increased seed arrival or increased seedling survival. However, 58% of seedling species found beneath tree canopies had no conspecific adult within 30 m, suggesting that the majority of seedling species were actively dispersed into the tree canopies (T.T.C, unpublished data).

Nine of the 11 seedling species found in the study were commonly cultivated in settled areas nearby. Only two species (*Syzygium cuminii* and *Azadirachta indica*) were shared between the present study and a previous study of a less disturbed dry forest vegetation upstream on the Tambiraiparani River[19]. This difference is striking considering the short distance (less than 1 km) from the Kalakad–Mundanthurai Tiger Reserve, a protected forest, to the trees sampled in this study. The lack of forest species could reveal a limitation of the seed-dispersing birds and bats that are common in the disturbed study site. The animals responsible for dispersing seeds in the village areas may forage exclusively near human settlements, precluding a role as vectors for seed movement from the forest. However, previous research in agricultural landscapes of South India has shown that structural complexity of vegetation improves the ability to retain bird species present in the native forests[20]. If denser patches of vegetation are allowed to form around isolated trees, a greater diversity of seed-dispersing animals may start using the trees as a food resource, improving connectivity between forest and anthropogenic habitat[17]. Our study reveals that many of the same tree species which are planted as saplings as part of reforestation programmes in the area occur naturally as seedlings under fig tree canopies. Additional reforestation efforts which take advantage of seed dispersal services provided by frugivores and focus on protecting naturally recruited seedlings beneath fig trees may be a cost-effective addition to direct planting of saplings. If *Ficus* are allowed to grow in fallow land within village limits, where there is a high chance of natural afforestation, the woody vegetation beneath those *Ficus* trees may provide villagers with fuel wood, fodder and medicinal plants, resources which are currently scarce in the landscape.

Effective biodiversity conservation in the 21st century should involve local people and maintain ecosystem processes in human-inhabited areas. Recent research on sacred groves has shown that incorporating local religious traditions into biodiversity conservation is one way to accomplish these goals. The same cultural traditions that have protected sacred groves have preserved individual remnant trees, which also have the potential to support wild plants and animals. A combination of public policy, science and religious leadership could protect recruiting tree seedlings beneath these isolated trees, eventually leading to improved wildlife habitat and a sustainable source of plant resources for local people.

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