INFLUENCE OF FOREST COVER ON FRUIT AND FRUGIVORE RICHNESS AND ABUNDANCE IN SOUTHERN WESTERN GHATS

Dissertation submitted to the

Saurashtra University, Rajkot

In partial fulfilment of

Master's Degree in Wildlife Science

By

Patel Zankhnaben Thakorbhai

Under the Supervision of

Dr. Amit Kumar

Dr. Rohit Naniwadekar

July, 2021

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

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CERTIFICATE

This is to certify that **Patel Zankhnaben Thakorbhai** has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science of the Saurashtra University, Rajkot, Gujarat. The topic of her dissertation is **'Influence of forest cover on fruit and frugivore richness and abundance in southern Western Ghats'.** The study was carried out under our supervision from January 2021 to June 2021. We hereby certify that this work has not been submitted for any degree to any university.

Dr. Amit Kumar
Scientist C
Wildlife Institute of India
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Date: 17-08-2021
Place: Dehradun

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DECLARATION

I, **Patel Zankhnaben Thakorbhai**, hereby declare that the research work entitled **'Influence of forest cover on fruit and frugivore richness and abundance in southern Western Ghats'** carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Dr. Amit Kumar** at the Wildlife Institute of India and **Dr. Rohit Naniwadekar** of the Nature Conservation Foundation from January 2021 to June 2021. I hereby declare that this work has not been submitted for any other degree of any university.

Date:
Place: Dehra Dun

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CERTIFICATE OF PLAGIARISM CHECK

It is certified that the M.Sc thesis titled **'Influence of forest cover on fruit and frugivore richness and abundance in southern Western Ghats'** submitted by Ms. Patel Zankhnaben Thakorbhai has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

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SUMMARY

Habitat fragmentation is a pervasive threat to ecosystem processes like seed dispersal, which is vital for biodiversity maintenance in tropical forests. Habitat fragmentation negatively impacts the richness, abundance and composition of plants and animals, thereby disrupting the interactions between them, with cascading impacts on biodiversity. However, the remnant fragments continue to harbour biodiversity. However, it is critical to determine the functional value of the fragments in terms of fruit resource diversity and availability and prevalence of frugivores across different size classes. To this end, I conducted the study in the Valparai plateau and adjacent contiguous patches of rainforests in the Western Ghats. I first determined the organization of plant-seed disperser community and identified key frugivores and plants in the landscape using network analysis. Using mixed models and the recently developed Joint Species Distribution Modelling approach called HMSC (hierarchical modelling of species communities), I investigated 1) the relationship between the amount of forest cover and richness of fruiting plants across different seed size classes, 2) the relationship between the amount of forest cover and availability of fruits across different seed size classes 3) the relationship between richness and presence of all the avian frugivores and, amount of forest cover, and richness and availability of fruits. I recorded the frugivores and fruiting plants from 33 trails distributed in 12 fragments and 2 sites in contiguous area during four months of sampling. I also recorded plant-frugivore interactions. I documented 49 species of fruiting plants and 17 species of avian frugivores and three species of mammalian frugivore between January – May 2021. Network analysis revealed five species of figs and regional endemic frugivores, like the Malabar Gray Hornbill, Yellow-browed Bulbul, White-cheeked Barbet as key members of plant-seed disperser community. Though the explained variation was low, I found a positive relationship between fruit availability of medium-seeded species and the amount of forest cover and negative relationship between fruit availability of small-seeded species and the amount of forest cover. I did not find any relationship between fruit availability of large-seeded plants and forest cover. The overall diversity of frugivores was not associated with forest cover or fruit availability. Large-bodied and wide-ranging frugivores, like Imperial-Pigeons and hornbills, exhibited positive association with forest cover, while regional endemic frugivores exhibited positive relationship with richness of fruiting plants. This study demonstrates that small fragments, albeit with some alterations, can continue to contribute valuable resources to frugivores and harbor significant biodiversity in an otherwise resource-poor fragmented landscape.

INTRODUCTION

Tropical forests cover about 6% of the total world's land area and harbor more than 50% of species diversity (FAO, 2020). Up to 90% of tropical plants are dependent on animals for dispersing the seeds (Howe and Smallwood, 1982; Jordano et al., 2002). Fleshy-fruited plants support most of the vertebrate biomass in tropical forests (Terborgh, 1992). Frugivores that effectively disperse seeds of plants play an important part in the maintenance of plant diversity (Terborgh, 1992). Dispersal of seeds is critical for enabling the escape of the seed from the density-dependent mortality factors under the parent tree (Janzen, 1970). Additionally, plant-frugivore interactions play a considerable role in the species diversification of plant and vertebrate species, enabling the maintenance of diversity in tropical forests (Fleming and Kress, 2011). Variation in availability of resources over space and time affect plant-seed disperser interactions. Plant-seed disperser interactions are constrained by species-specific traits such as fruit size, gape width and body mass (Hagen et al., 2012). For example, large-bodied frugivores are generally identified as crucial dispersers of large-seeded plants (Naniwadekar et al., 2019a). Morphological constraints (e.g. small gape width of birds) of small- and medium-bodied frugivores allow them to disperse seeds of mostly the small and medium-seeded fruits. Intact forests support species-rich communities and diverse plant-frugivore interactions. Unfortunately, anthropogenic activities are responsible for the loss and fragmentation of these intact forests, thereby affecting the abundance and composition of different taxonomic groups, including plants, invertebrates and vertebrates (Haddad et al., 2015).

Fragmentation can negatively impact fruit availability (Morante-Filho et al., 2018). Fragmentation negatively impacts the density and richness of old-growth plant species (Osuri et al., 2017). Large-seeded plants are often absent in the smaller fragments (Cramer et al., 2007). Large-bodied frugivores are also affected negatively by fragmentation (Cramer et al., 2007; Emer et al., 2018). The functional richness of frugivorous birds is negatively affected due to the decline in patch size (Bovo et al., 2018). The functional contribution of key seed dispersers declines in fragmented forests (Marjakangas et al., 2020).

Given the altered composition of plants and animals in the fragments, mutualistic interactions between plants and animals, like seed dispersal, can be expected to be altered (Bregman et al., 2015; Hagen et al., 2012). Mutualistic interactions between plants and seed dispersers are disrupted by habitat disturbance (Magrach et al., 2014). Galetti et al. (2006) report reduced dispersal of the animal-dispersed palm species in small defaunated forest fragments, which results in low seedling densities and decreased regeneration of the species. Habitat fragmentation reduces the number of species visiting fruiting trees (Kirika et al., 2008). The proportion of interactions provided by frugivores are fewer in fragmented forests as compared to contiguous forests (Marjakangas et al., 2020). Limited evidence points towards a significant turnover in interactions across fragments (Emer et al., 2018; Jain et al., 2021). Additionally, there is a greater prevalence of interactions with small-seeded and open forest species in the fragments as compared to contiguous forests (Farwig et al., 2017; Jain et al., 2021). The proportion of forest-dependent species decreases due to reduction in patch size and increasing edge effect

(Morante-Filho et al., 2018). As a consequence, habitat fragmentation impacts seed removal rates negatively, and alters the seed dispersal distances (Lenz et al., 2011; Markl et al., 2012; McConkey et al., 2012). However, there is also evidence to the contrary. Reduced forest cover had a negative impact on the small-seeded Persea, but not so much on the large-seeded Myristica.(Gopal et al., 2020). Albeit compositional turnover in interactions, medium-sized fragments had similar diversity of interactions as compared to a contiguous forest site (Jain et al. 2021). This highlights the biodiversity and functional value of forest fragments.

Most of our understanding of the impacts of habitat fragmentation on plant-seed disperser interactions is from Neotropics (Berens et al., 2014; Cazetta et al., 2019; Emer et al., 2018; Galetti et al., 2006; Marjakangas et al., 2020). Very few studies are from Asian tropics (Gopal et al., 2020; Jain et al., 2021). Furthermore, most studies have focused on few plant species (Cazetta et al., 2019; Farwig et al., 2017; Gopal et al., 2020; Herrera and García, 2010; Kirika et al., 2008), and community-level studies have only now started emerging (Emer et al., 2018; Marjakangas et al., 2020; Jain et al., 2021). Additionally, given the compositional changes in plant communities due to fragmentation, the changes in fruit resource availability (richness and abundance) and its cascading influence on frugivores are poorly understood (but see Morante-Filho et al., 2018). Given that the members of the frugivore community vary in body size, different frugivore species may respond to different factors (e.g. fragmentation, fruit availability) at different scales (Carlo et al., 2013; García et al., 2011). This aspect that has been relatively poorly studied.

While many studies are trying to unravel the impact of fragmentation on biodiversity and its processes, the views pertaining to the interpretation of fragmentation are being debated for the past few years (Didham et al., 2012; Fahrig, 2021, 2019, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Saura, 2021a, 2021b). Fahrig (2013) defines fragmentation as a landscape-level process, but studies carried out in the field of fragmentation are generally focused at the patch level. Inferences drawn from such studies, while helpful, do not necessarily allow interpretation of the impacts of habitat fragmentation. Fahrig (2013) proposed that the amount of habitat within the landscape and not the configuration (patch size and isolation) is the primary driver of species responses. This was termed as the 'Habitat Amount hypothesis' (HAH) (Fahrig, 2013). A number of studies have found full or partial support for the HAH (De Camargo et al., 2018; Melo et al., 2017; Torrenta and Villard, 2017; Vieira et al., 2018). While other studies have failed to find evidence for the HAH but found support for patch size and isolation (Evju and Sverdrup-Thygeson, 2016; Haddad et al., 2017; Seibold et al., 2017). In my study, I have focused on the extent of forest cover (habitat amount) around my sampling unit to see the impacts of forest fragmentation on the community of fleshy-fruited plants and frugivores in the southern Western Ghats.

In contrast with past studies that have focused on seeing the impact of forest cover on a select number of species (Cazetta et al., 2019; Farwig et al., 2017; Gopal et al., 2020; Herrera and García, 2010; Kirika et al., 2008), I aimed to understand the influence of forest cover on the plant-seed disperser community in Southern Western Ghats. Additionally, I evaluated the impacts of forest cover on diversity and availability of fruits, an aspect little explored in the literature. The specific objectives of my study were to 1) evaluate the impact of forest cover on richness and availability of fruits, 2) determine the impact of forest cover and fruit availability on the diversity of frugivores, and 3) determine the species-specific responses of frugivores to forest cover, and fruit diversity and availability. To this end, I first described the organisation of the plant-seed disperser community using network analysis. I predicted that forest cover will 1) negatively impact the richness and availability of small-seeded plants, and positively impact medium and large-seeded plants, 2) positively impact the diversity of frugivores and species-specific responses of frugivores in the landscape. Given that the frugivores track fruit resources, I also expected a positive influence of fruit diversity and availability on frugivores.

STUDY AREA

I conducted the study in the Anamalai Tiger Reserve (958 km^2, Location: 10°12′–10°35′N, 76°49′–77°24′E) and the Valparai plateau (220 km^2, Location: 10°15′–10°22′N, 76°52′–76°59′E) in the Anamalai Hills of southern Western Ghats, Tamil Nadu. The study area comes under the Western Ghats - Sri Lanka biodiversity hotspot (Myers et al., 2000). It is amongst the most densely populated biodiversity hotspots globally (Cincotta et al., 2000). While the elevation in the study area ranges from 200 m to 2,500 m ASL, the present study was conducted in the mid-elevation range between 600 m to 1,500 m ASL. The forests of the intensive study area are classified as mid-elevation tropical wet evergreen forests of the *Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type (Pascal et al., 2004). The region receives 3,000 – 3,500 mm of rainfall during the south-west monsoon between June to September and in the north-east monsoon from October to January. The major part of the study was conducted in the Valparai plateau, which was once a contiguous rainforest. Large-scale deforestation and land-use changes from 1800 to 1940s modified the contiguous rainforest into ~45 remnant rainforest patches, varying in area from 1 ha to 300 ha (Mudappa and Raman, 2007; Osuri et al., 2019). The rainforest fragments on the Valparai Plateau (4.5% of the plateau area) are surrounded by the matrix of tea (51% of the area), coffee (11% of the area), cardamom and/or *Eucalyptus* plantations (Mudappa and Raman, 2007). Relatively undisturbed forests, namely the Anamalai Tiger Reserve (958 km^2), the Parambikulam Tiger Reserve (634 km^2), and the Vazhachal Reserved Forest (413.95 km^2)

surrounds the Valparai plateau. The most common trees in the forests are *Palaquium ellipticum* (Sapotaceae), *Mesua ferrea* (Clusiaceae), *Vateria indica* (Dipterocarpaceae), *Cullenia exarillata* (Malvaceae), *Reinwardtiodendron anamallayanum* (Meliaceae), *Drypetes malabarica* (Putranjivaceae) and *Antidesma menasu* (Stilagenaceae). The understory has various climbers and shrub species (Muthuramkumar et al., 2006). The rainforest fragments have at least 18 species of *Ficus* (Pawar et al., 2021). This area has about 28 species of mammals, including tiger *Panthera tigris*, leopard *Panthera pardus*, Asiatic elephants *Elephas maximus*, gaur *Bos gaurus*, lion-tailed macaques *Macaca silenus*, Nilgiri langur *Trachypithecus johnii*, Malabar giant squirrel *Ratufa indica*, to name a few (Sridhar et al., 2009). This area is also important for many bird species, including the Great Hornbill *Buceros bicornis*, Malabar Gray Hornbill *Ocyceros griseus*, Malabar Trogon *Harpactes fasciatus*, Malabar Woodshrike *Tephrodornis sylvicola*, White-bellied Blue Flycatcher *Cyornis pallidipes*, Black-and-Orange Flycatcher *Ficedula nigrorufa,* among others (Raman, 2006). Some of the frugivores in the landscape are Malabar Gray Hornbill *Ocyceros griseus*, Mountain Imperial-Pigeon *Ducula badia*, Yellow-browed Bulbul *Iole indica*, Southern Hill Myna *Gracula indica*, White-cheeked Barbet *Psilopogon viridis* and primates like the Lion-tailed Macaque *Macaca Silenus*, Nilgiri langur *Trchypithecus johnii* and Bonnet Macaque *Macaca radiata* (Gopal et al., 2020).

I selected 14 rainforest patches in the study area, including 12 rainforest fragments across different sizes (2-275 ha) and two sites in contiguous forest areas (Table 1; Fig. 1). Private plantation companies own all the sampled fragments. The contiguous forest patches are part of the Anamalai Tiger Reserve (Table 1).

Table 1. ***List of the study sites and their area. Number of transects in each site***

Name of the site	**Size (ha)**	**No. of transects**
Rainforest fragments		
Selaliparai 1	1.89	1
Varattuparai 4	3.27	1
Varattuparai 1-3	12.23	2
Vellonie	13.93	1
Murugalli Blackbridge	15.43	1
Old Valparai	36.35	3
Murugalli Hospital	37.21	2
Pannimade	90.07	2
Iyerpadi top	90.20	3
Murugalli Sholayar	100.14	3
Candura	100.99	3
Kalyanpandal	274.41	4
Contiguous forest - Anamalai Tiger Reserve		
Manamboli	-	3
36 & 37 HPB	-	4

Figure 1. Map of the Valparai plateau (orange outline). The sampled rainforest patches are shown (white outline). Each patch had 1-4 trails based on the area of the patch. I sampled 33 transects (300 m in length) across 14 patches

Figure 2. Great Hornbills flying over a rainforest fragment in Valparai. Painting: Sartaj Ghuman

Figure 3. Rainforest fragment in Valparai surrounded by matrix of tea. © Ganesh Raghunathan

Figure 4. Edge of rain forest fragment. Picture showing active use of tea plantations by large herbivores.

METHODS

I marked 33 trails in 12 rainforest fragments and 2 sites in contiguous forest (Fig. 1, Table 1). Each trail was 300 m in length. This was the longest trail that I could mark in the smallest fragment (~ 2 ha). The number of trails in a fragment varied between one to four according to the forest patch size (Fig. 1, Table 1). In fragments with multiple trails, trails were separated by a distance of at least 100 m. I monitored these trails for five sessions to estimate fruit and frugivore richness and abundance between January to May 2021. In every session, each of the 33 trails was walked once.

Richness and abundance of fruiting plants

I recorded the species identity and the number of all plants (trees, shrubs and/or climbers) with ripe, fleshy fruits at a distance of 10 m at either side of the trail (300 × 20 m). I counted the number of ripe fruits in the visible part of the canopy and then extrapolated it to the entire canopy of the plant, following Davidar and Morton (1986). For a few species, where ripe and unripe fruits could not be distinguished (e.g. *Cryptocarya wightiana*, certain *Ficus* spp.), I estimated the entire fruit crop for that individual plant.

Richness and abundance of frugivores

I used variable-width transects for determining the richness and abundance of frugivores. I walked the trails in the morning (0600 - 1030 hr) and late afternoon (1400 - 1730 hr), which corresponds to the peak activity time of frugivores (Gopal et al., 2020; Naniwadekar et al., 2019a). I recorded species identity, the number of individuals and the perpendicular distance of the bird/mammal from the trail on sighting an animal during trail walk.

Richness and frequency of plant-frugivore interactions

I recorded the plant-frugivore interactions during and outside (opportunistic observations) the trail walks. On encountering frugivore/s on a fruiting tree, I recorded the identity of the plant and frugivores, and the number of individuals of the frugivore species following Naniwadekar et al. (2021).

Morphological traits

At least 10 fruits of the plant on which interactions were recorded were measured for its dimensions. I measured fruit width, fruit length, seed width and seed length using vernier calliper. I classified the seeds as small-seeded, medium-seeded, and large-seeded, following Naniwadekar et al. (2019a).

ANALYSIS

Organisation of the plant-seed disperser communities

I generated a bipartite plant-seed disperser interaction network based on all the interactions of fruiting plants and their diurnal seed dispersers (including birds and mammals). I created a weighted interaction matrix of plants (rows) and seed-dispersers (column). The number of frugivores seen on fruiting plants were considered as weights in the network. I considered only those frugivores that were observed swallowing seeds at least once as legitimate seed dispersers for a particular plant species. I estimated different network-level metrics and species-level metrics.

At the network level, I estimated connectance, nestedness (weighted NODF), specialisation (*H’*), generality and vulnerability to determine the structure of the seed-disperser community. Connectance is the proportion of realised interactions out of total possible interactions. Nestedness value ranges from 0 to 100, with a higher value indicating greater nestedness. A community is highly nested when the specialist species mostly interact with generalist species. Higher nestedness values indicate a more robust community indicating the central role of generalist species that is connected with specialist species (Bascompte and Jordano, 2007). Specialisation is the measure of selectivity among different species in interaction partnerships (García, 2016). The greater the selectivity of the species, the greater is the specialisation of the network. It ranges from 0 to 1, wherein 1 indicates complete specialisation and 0 indicates a generalized community. Generality is the mean number of plant partners for seed dispersers. Vulnerability is the mean number of seed dispersers for plants. Plant-seed disperser community is often organized into modules (sub-communities) wherein species within a module interact more with each other than species across the modules. I also determined weighted modularity in the plant-seed disperser network. Modularity shows the number of subgroups (modules) in the network. Modularity value ranges from 0 to 1 (0 indicating less modular and 1 indicates complete modularity) (García, 2016).

At the species-level, I estimated degree and species strength. Degree is the number of mutualistic partners of the focal species. Species strength is the measure of quantitative importance of a species for the other level (seed disperser or plant). It explains the relative importance of species in comparison to other species in the network. Higher the species strength higher the importance of species in the network.

I determined the significance of observed connectance, nestedness, specialization and modularity by comparing the observed value with 1000 randomly generated networks constructed using the method ‘r2dtable’ (which randomizes the interactions by keeping the marginal row and column total same as the observed matrix). I carried out all the analysis in R package “bipartite” (Dormann et al., 2008).

Selection of landscape variables

I initially aimed to use patch size and habitat amount as landscape variables. I measured the patch size of each of my study sites using previously classified GIS images of the study area (Gopal et al., 2020; Wordley et al., 2015). These classified images demarcate the extent of forest cover in the landscape

(Wordley et al., 2015). I estimated habitat amount by determining the forest cover in a fixed radius around the midpoint of the transect. To objectively determine the buffer radius around the transect, I followed the multi-scale analysis approach outlined by Fahrig (2013) and implemented in Magioli et al., (2021). As per this method, the relationship between species richness and habitat amount is evaluated at different buffer radii. The scale at which the relationship of species richness and habitat amount is most strongly associated is selected as a scale of effect. Following this method, I calculated habitat amounts (extent of forest cover) at 100, 200, 300, 500, 1000, 1500 and 2000 m radius. I used QGIS for retrieving data on forest cover and patch size.

Influence of landscape predictors on ripe fruit richness and availability

To analyze the influence of landscape variables on fruit richness and availability, I used Linear Mixed-effects Models. I aimed to use patch size, percentage forest cover around each transect at the scale of 300 m and 1500 m as predictor variables (see section 'Optimum scale for estimating habitat amount' in result for explanation to use these predictor variables). Percentage forest cover around the transect was calculated from the amount of forest cover in a radius of 300 m and 1500 m from the mid-point of the transect. Patch size and percentage forest cover around each transect (at the scale of 300 m and 1500 m) was strongly correlated ($r > 0.79$). Habitat amount at 300 m scale and 1500 m scale were moderately correlated ($r = 0.65$). Given that frugivores are known to track resources at different spatial scales, I used percentage forest cover at 300 m and 1500 m scale as predictor variables. I standardised the predictor variables to compare the relative influence of two predictors on the response variables. I used the Generalised Linear Mixed-effects Model (GLMM) with Poisson error structure (as richness is a count data) to examine the influence of the two predictor variables on 1) overall fruiting plant richness, 2) richness of small-seeded plants 3) richness of medium-seeded plants and 4) richness of large-seeded plants. None of the models was overdispersed. I used a linear mixed-effects model (LMM) with Gaussian error structure to determine the influence of the two predictor variables on 1) overall fruit availability, 2) availability of small-seeded plants 3) availability of medium-seeded plants, and 4) availability of large-seeded plants. Since each transect was walked five times, I defined 'transect ID' as the random effect for the GLMMs and LMM. I used R packages 'nlme' and 'glmmTMB' for the analysis (Brooks et al., 2017; Pinheiro et al., 2012).

Influence of landscape predictors, fruit plant richness and fruit availability on frugivore diversity

To analyze the influence of landscape variables, fruit richness and availability on richness and abundance of frugivores, I used the Linear Mixed-effects Model and Hierarchical Modelling of Species Communities (HMSC) i.e. the joint species distribution modeling approach (Ovaskainen et al., 2017).

I used the Generalised Linear Mixed-effects Model (GLMM) with Poisson error structure to determine relationship between frugivore species richness and the four predictor variables, namely forest cover in 300 m, forest cover in 1500 m, fruit richness and fruit availability. Since each transect was walked five times, I defined ‘transect id’ as the random effect.

HMSC uses trait and phylogenetic relationship data to explain the response of species to different species-specific covariates. The HMSC framework includes occurrence/abundance data of species in sampling units (Y matrix), environmental data (X matrix), trait data (T matrix) and phylogenetic data (C matrix) (Fig. 5).

I included data of 16 avian frugivore species (Y matrix) collected over 165 sampling units, i.e. 33 transects walked five times each. The species with less than five detections during the study period were excluded from analysis following Ovaiskanen et al. (2017). As environmental covariates, I used percentage forest cover in 300 m radius around each transect, percentage forest cover in 1500 m radius around each transect, fruit plant richness and log-transformed fruit availability (X matrix). For the frugivore trait data, I used scores of Principal Component Analysis performed on nine morphological traits of birds (including body mass, beak, wing and tarsus measurements) by Pigot et al. (2020). Since I was analysing the data for only frugivorous birds, I used only four of the nine PC components (PC1, PC3, PC5, PC8) that best explained the morphospace occupied by frugivores (see Extended Dat Fig. 8C in Pigot et al. 2020). PC1 is associated with body mass, PC3 with beak width and depth, and tail length, PC5 with tarsus length and PC8 with two different measures of beak length (see Extended Data Fig. 3 in Pigot et al. 2020). The phylogenetic tree (C matrix) information was retrieved from www.birdtree.org. I obtained 100 trees from a posterior distribution of

10000 trees based on Ericson All Species backbone phylogeny with 9,930 OTUs for 16 bird species (Jetz et al., 2012). The HMSC framework uses Bayesian inference and Markov Chain Monte Carlo (MCMC) estimation to assess the focal community responses. I did not use mammal data for this one as I did not have comparable information on traits and phylogeny.

I ran four HMSC models. Two models (count data) were fitted with log-normal Poisson distribution. This included one global model (with all covariates) and one random-effects only model (with no covariates). I also fitted two (presence-absence data) models with Probit distribution, 1) the global model (with all covariates) and 2) random-effects only model (with no covariates). I sampled posterior distribution with four Markov Chain Monte Carlo (MCMC) chains. The total number of iterations was 3,750,000 which included 1,260,000 transients (sample size per chain = 250, thinning interval = 10000). I examined the MCMC convergence by examining potential scale reduction factors (PSRF) of model parameters (Gelman and Rubin, 1992). The PSRF value of model parameters less than 1.05 indicates model convergence (Ovaskainen et al., 2017). I compared the global model with the random-effects model using the Widely-applicable Akaike Information Criterion (WAIC) (Watanabe et al. 2010).

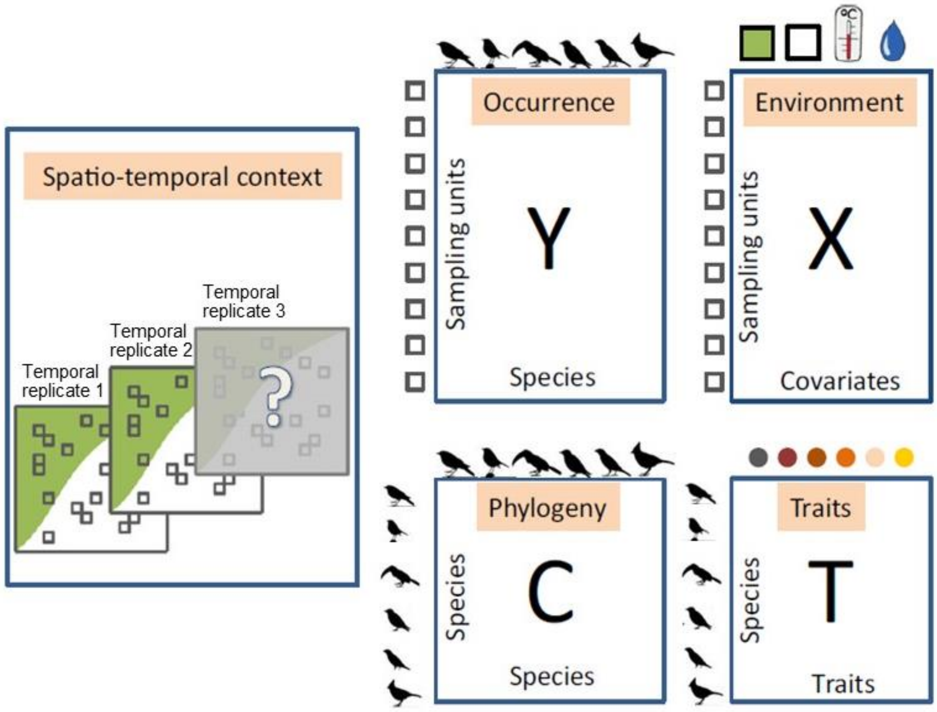

Figure 5. Schematic framework of HMSC (adapted from Ovaskainen et al. (2017)). Y matrix - species occurrence in sampling units, X matrix - environmental covariates, T matrix - Traits of study species, C matrix - Phylogenetic relationship tree of study species.

RESULTS

Plant-seed disperser interactions

I recorded 437 interactions between 35 plant species and 18 diurnal frugivores (15 birds and three mammals) species. Amongst 437 interactions, 93 interactions were unique pairwise interactions. I documented 177 interactions during trail walks and 260 interactions opportunistically outside trail walks. Out of 437 interactions, 204 (47.1%) interactions were observed on eight species of *Ficus*, 163 interactions on 17 species of trees, 61 interactions on six species of shrubs and nine interactions on four species of climbers. Of total interactions, maximum number of interaction were observed for Red-whiskered Bulbul (72), followed by Southern Hill Myna (58), White-cheeked Barbet (58), Malabar Gray Hornbill (51) and Asian Fairy blue bird (35). Although major proportion of Red-whiskered Bulbul's interactions was with *Lantana camara.*

Community-level Properties

Network analysis revealed that the observed network was less connected and nested, and more specialised than the null community (Table 2). The mean number of frugivore species partners per plant species (generality) was 5.2, and the mean number of plant species partners per frugivore species (vulnerability) was 3.6. The observed community was more modular than the null community (Table 2). Modularity analysis identified eight different modules (Fig. 6). The largest module comprised of figs (e.g. fiam, fiti), barbets (maba, wcba), Great Hornbill (grho) and Asian Fairy Bluebird (afbl). The three mammal species (nila, boma, mgsq) and Malabar Grey Hornbill (mgho) were in the first two modules, and they interacted with several medium (e.g. *Persea macrantha*) and large-seeded (e.g. *Litsea oleoides*) species, including some figs.

Table 2. Observed values of network-level metrics and the mean and SD as obtained from the 1000 null models. Z-scores greater/less than 1.96 indicate a significant departure of the observed metrics from the null communities.

	Observed value	**Null mean**	**Null SD**	**Z score**
Connectance	0.148	0.275	0.006	-19.6
Specialization	0.520	0.102	0.009	45.8
Weighted NODF	18.176	37.257	2.501	-7.6
Modularity	0.52	0.171	0.0109	32.0

Species-level Properties

Five species of *Ficus* had high species degree values (number of seed disperser partners) along with the *Flacourtia montana* (5 species), *Glochidion ellipticum* (5 species) and *Persea macrantha* (5 species) (Table 3). Malabar Gray Hornbill had the highest species degree (18 species), followed by White-cheeked Barbet (14 species), Yellow-browed Bulbul (12 species), Red-whiskered Bulbul (9 species) and Asian Fairy Bluebird (6 species) (Table 3). Among mammals, Malabar Giant Squirrel was observed feeding on the maximum number of plant species (6 species). I observed the squirrel predating on the seeds of *Artocarpus heterophyllus,* and I was not certain whether the squirrel was dispersing or predating seeds of *Myristica dactyloides*. Therefore, these two plant species were not included in the degree calculations for the squirrel.

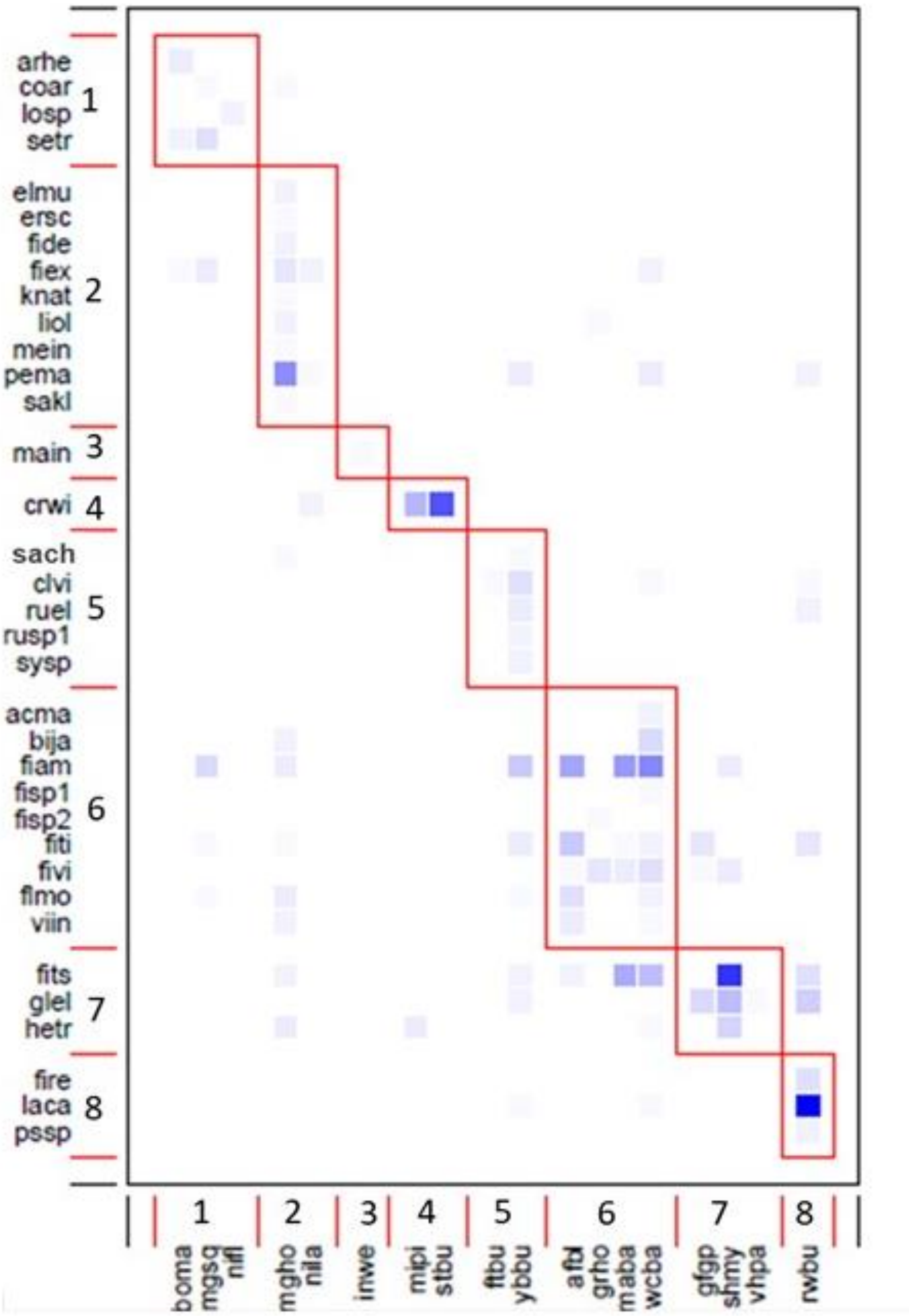

Figure 6. Figure showing eight different modules (35 plant species and 18 frugivore species) in red boxes. Plant species are in rows and frugivores are in columns. Full names of the species are listed in Appendix 2 and 3.

Table 3. Observed value of two species-level metrics of plants and frugivores. Degree is the number of partners and species strength is the measure of importance of the species for its partners. The bold numbers indicated highest species degree.

Group	**Species**	**Degree**	**Species strength**
Plant	*Ficus tinctoria*	8	0.906
	Ficus amplissima	7	**1.987**
	Ficus tsjahela	7	1.400
	Ficus virens	6	1.010
	Ficus exasperata	5	0.856
Frugivore	*Ocyceros griceus* Malabar Gray Hornbill	18	**9.835**
	Psilopogon viridis White-cheeked Barbet	14	4.381
	Iole indica Yellow-browed Bulbul	12	4.281
	Pycnonotus jocosus Red-whiskered Bulbul	9	4.069
	Irena puella Asian Fairy-bluebird	6	1.569
	Ratufa indica Malabar Giant Squirrel	6	1.670

Figure 7. Important rain forest avian frugivores of the study area identified from network analysis: a) Malabar Gray Hornbill b) White-cheeked Barbet c)Yellow-browed bulbul d) Asian Fairy bluebird. © a) Savithri Singh b) Aseem kothiala b) Rahul Singh d) Garima Bhatia

Optimum scale for estimating habitat amount

The relationship between overall species richness and varying amounts of forest cover peaked at around 300 m (Fig. 8). However, for the nine main frugivore species (across different groups varying in body size, including white-eye, barbets, myna, bulbul, imperial-pigeon, hornbill), the R^2 values peaked at different buffer radii. Generally, for the smaller frugivores (Nilgiri Flowerpecker, Indian White-eye, Yellow-browed Bulbul), the R^2 values peaked between 200-500 m and for few other frugivores (Malabar Gray Hornbill, Southern Hill Myna and Malabar Barbet), R^2 values peaked between 1500-3000 m. Therefore, I chose two radii (300 m, 1500 m) for estimating forest cover around the transect for further analysis. The amount of forest cover at the scale of 300 m around the transect was moderately correlated with 1500 m (r = 0.65; 95% CI: 0.39 – 0.81).

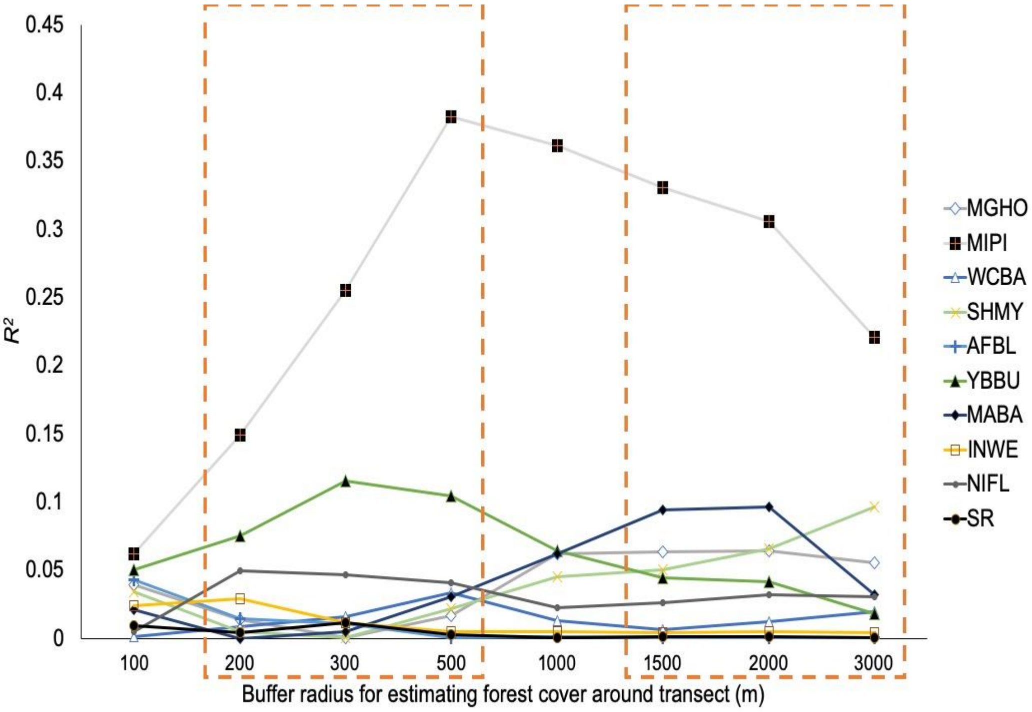

Figure 8. To determine the optimum radius for estimating forest cover, I used linear models to examine the relationship between the encounter rate of nine frugivore species and overall species richness (SR) with varying buffer radii (100 - 3000 m). The figure shows R^2 values for linear models for nine frugivore species and overall species richness. The R^2 values peaked at different radii for different species, but there were two prominent peaks (shown in red boxes), one at relatively smaller scales (200 - 500 m) for six species, and the other at large scales (1500 - 3000 m) for three species. MGHO - Malabar Gray Hornbill, MIPI - Mountain Imperial-Pigeon, WCBA - White-cheeked Barbet, SHMY - Southern Hill Myna, AFBL - Asian Fairy Bluebird, YBBU - Yellow-browed Bulbul, MABA - Malabar Barbet, INWE - Indian White-eye, NIFL - Nilgiri Flowerpecker.

Fruiting plant richness and availability

I recorded 49 ripe-fruit bearing plant species during the study period (Table S1). Among the 49 species, 28 species were small-seeded (< 5 mm width), 12 were medium-seeded (5-15 mm width), and nine were large-seeded (> 15 mm width). The richness of small-seeded fruiting plant species was higher than medium- and large-seeded plant species (Fig. 9) as interpreted by non-overlapping bootstrapped 95% CI. The mean number of ripe fruits available was maximum for the small-seeded plants followed by medium- and large-seeded plants (Fig. 10).

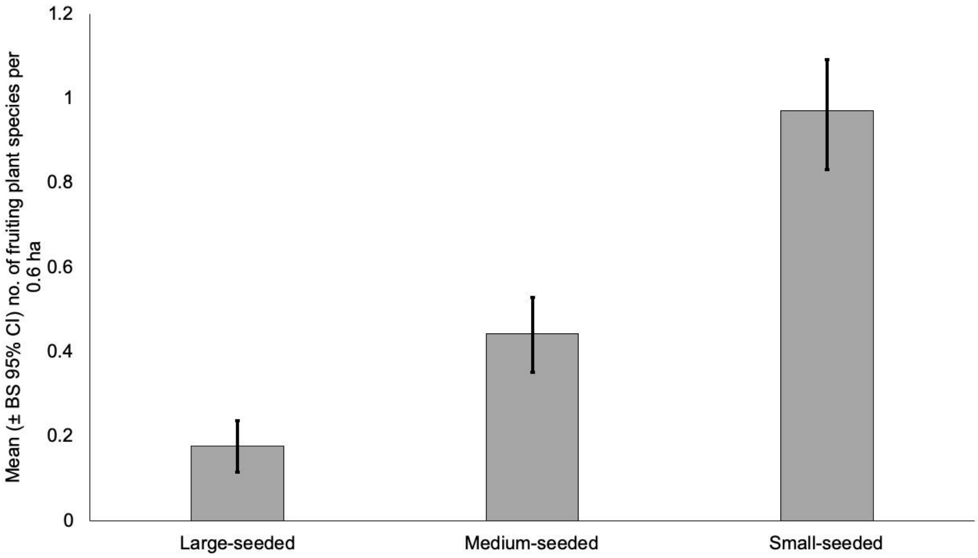

Figure 9. Mean (95% bootstrapped CI) number of fruiting plant species that were detected during each trail walk (plot area: 0.6 ha; 300 m x 20 m). The richness of small-seeded plants was higher as compared to medium- and large-seeded plants. Number of bootstraps = 9999.

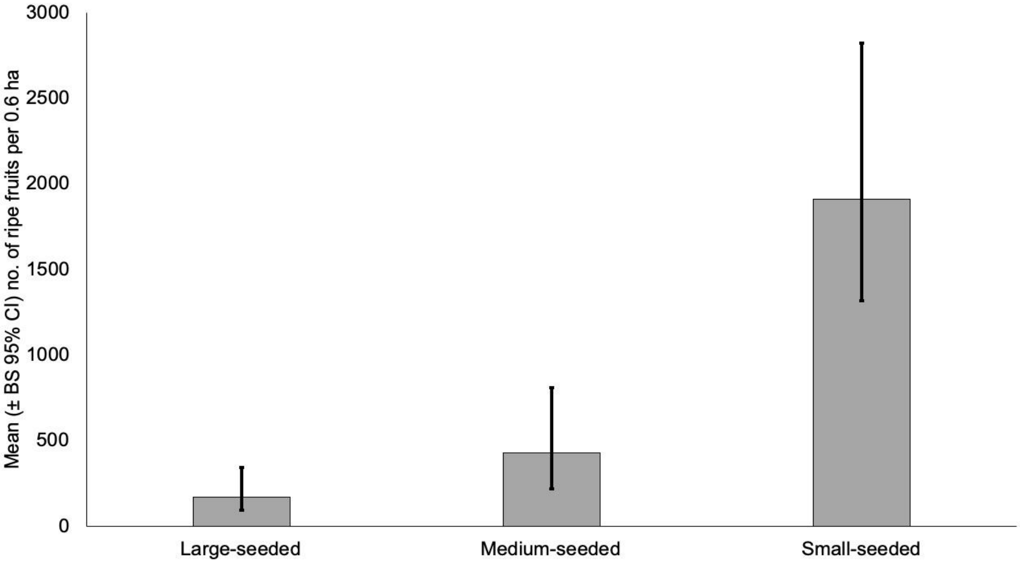

Figure 10. Mean (95% bootstrapped CI) number of ripe fruits that were estimated during each trail walk (plot area: 0.6 ha; 300 m x 20 m). The availability of small-seeded plants was higher as compared to medium- and large-seeded plants.

At the 300 m buffer radius scale, the richness of fruiting small-seeded plants was positively associated with forest cover (Fig. 11). However, forest cover explained little variation in species richness (marginal $R^2 = 0.023$). I did not find any relationship between species richness of medium- and large-seeded plants and habitat amount as the 95% CI overlapped zero (Fig. 11). At the 1500 m buffer radius scale, the richness of fruiting small-seeded plants was negatively associated with forest cover (marginal $R^2 = 0.023$, Fig. 11). On the other hand, the richness of medium-seeded plants was positively associated with forest cover (marginal $R^2 = 0.05$, Fig. 11). However, the associated marginal R^2 values were small, indicating only a small variation in species richness was explained by the forest cover.

At the scale of 300 m, forest cover did not influence the availability of different kinds of fruits (Fig. 12). However, at the scale of 1500 m, the availability of small-seeded fruits was negatively influenced by forest cover (marginal $R^2 = 0.11$; Fig. 12), while availability of medium-seeded fruits was positively influenced by forest cover (marginal $R^2 = 0.058$; Fig. 12).

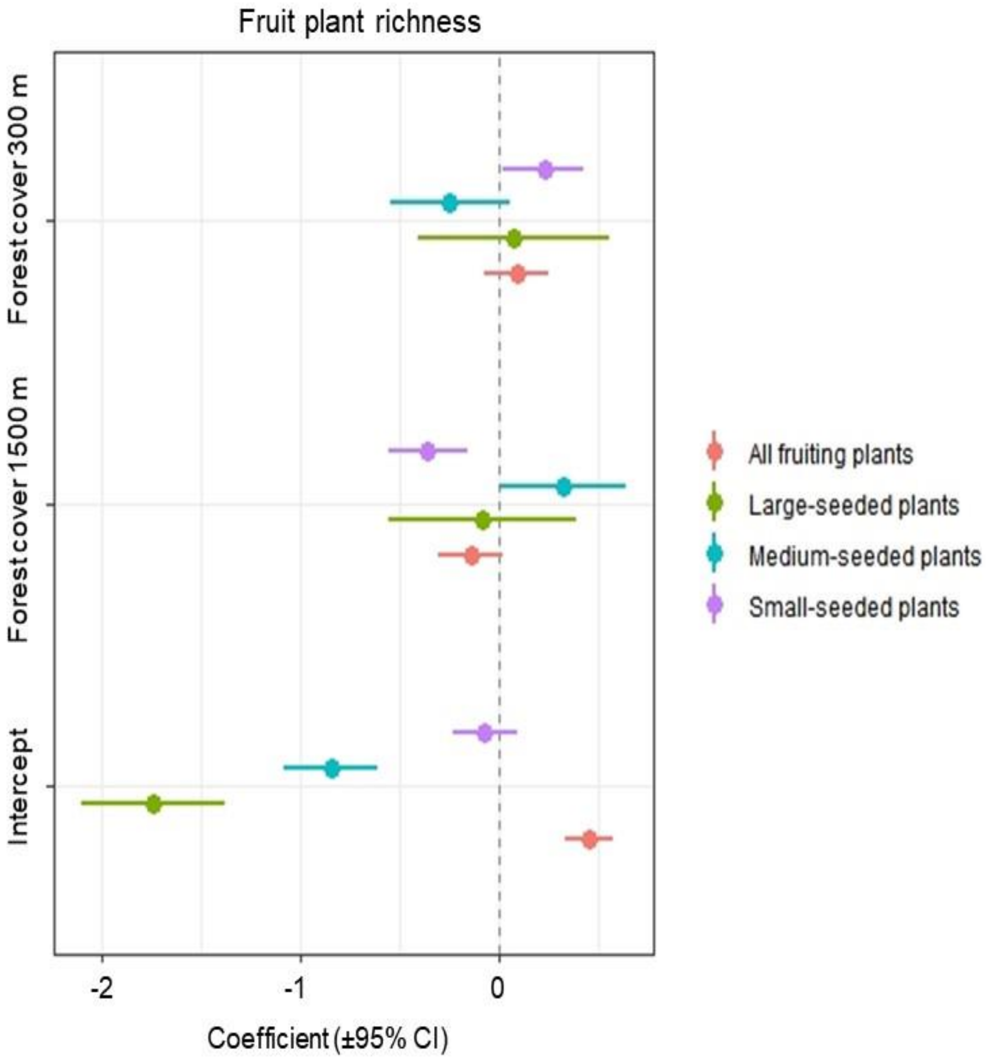

Figure 11. Coefficients and 95% CI for the amount of forest cover in the radius of 300 m and 1500 m estimated using GLMMs (Poisson-error structure) separately for all fruiting plants, small-seeded plants, medium-seeded plants and large-seeded plants. Predictor variables were standardised for the analysis. Coefficients whose associated 95% CI did not overlap zero were inferred to have statistically significant influence on the response variable.

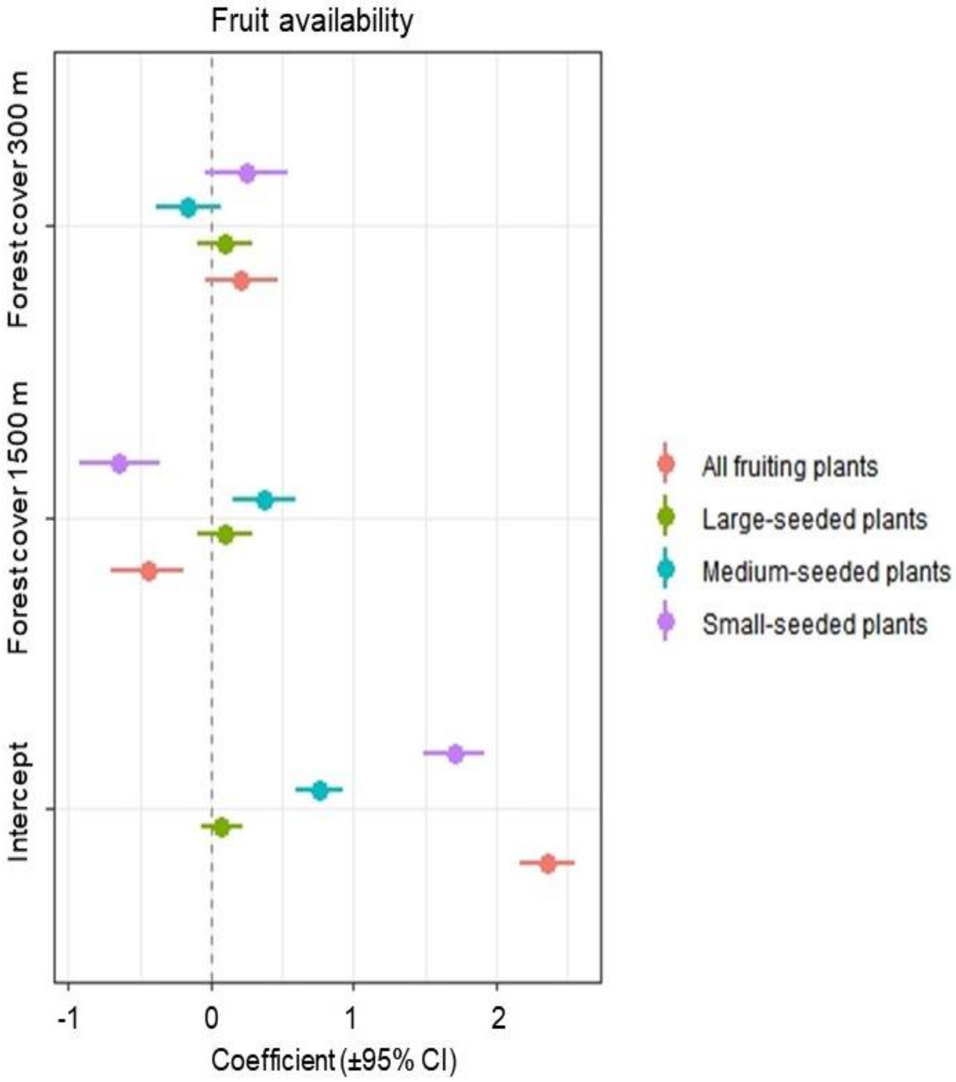

Figure 12. Coefficient 95% and CI for the amount of forest cover in the radius of 300 m and 1500 m estimated using LMMs (Gaussian-error structure) separately for the availability of all fruits, small-seeded fruits, medium-seeded fruits and large-seeded fruits. Predictor variables were standardised for the analysis. Coefficients whose associated 95% CI did not overlap zero were inferred to have statistically significant influence on the response variable.

Frugivore Richness and Abundance

I recorded a total of 17 species of avian frugivores during the study period. This included two species of barbets, three species of bulbuls, two species of hornbills, Mountain Imperial-Pigeon (Appendix 3). I did not find any relationship of frugivore richness with the covariates i.e., forest cover in 300 m and 1500 m radius, fruit plant richness and fruit availability (Fig. 13).

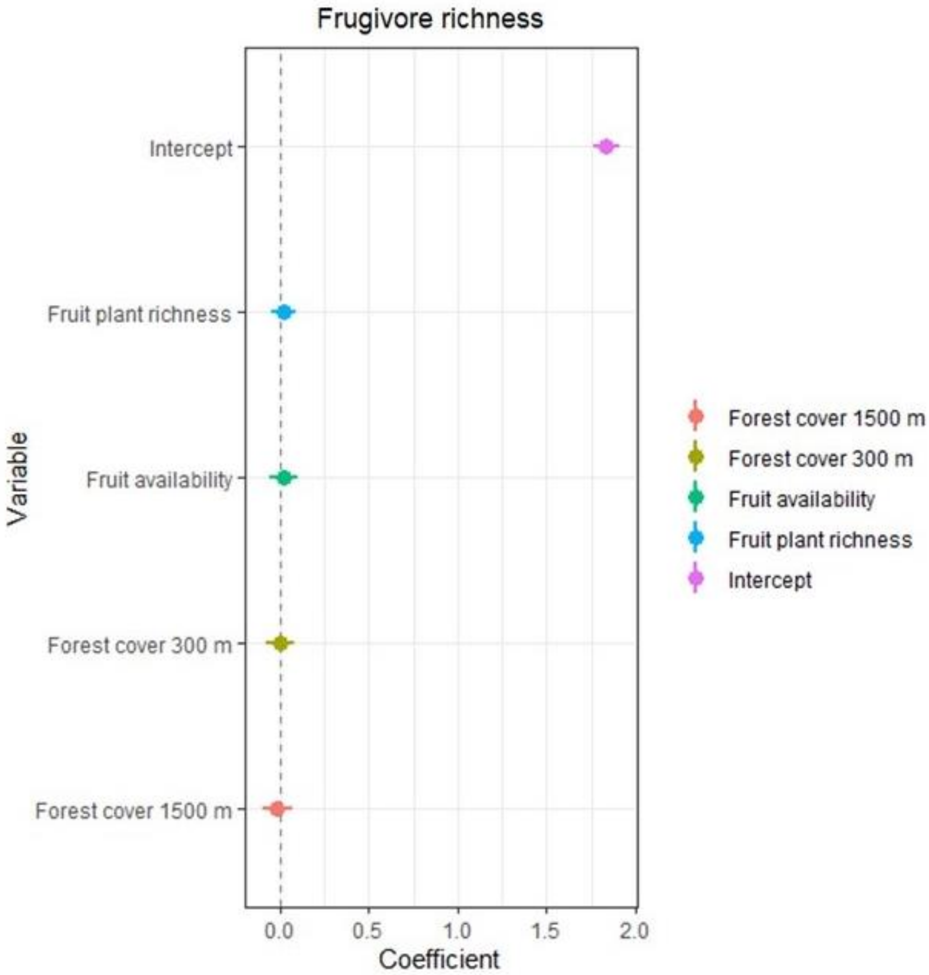

Figure 13. Coefficient and 95% CI for the amount of forest cover in the radius of 300 m and 1500 m, fruit plant richness and fruit availability estimated using GLMMs (Poisson-error structure). Predictor variables were standardised for the analysis. Coefficients whose associated 95% CI did not overlap zero were inferred to have statistically significant influence on the response variable.

I included 16 out of the 17 frugivore species in the HMSC analysis. One species was observed in less than five transects and was left out. I found that the WAIC value for the global abundance model was more than intercept-only model. However, for the presence-absence model, the WAIC value was much lower than the intercept-only model (WAIC (global model: presence-absence) = 7.5357; WAIC (intercept-only model: presence-absence) = 6967.41). Therefore, I interpreted the output for only the presence-absence model. The MCMC chain of the fitted presence-absence model had reached convergence after 2,500,000 iterations. The mean potential scale reduction factor (psrf) for β parameters (response of species to environmental covariates) was 1.00 (range: 0.9 – 1.02). The total explained variation in the presence-absence of different frugivores varied between 0.02 (Nilgiri Flowerpecker) to 0.299 (Red-whiskered Bulbul) (Fig. 14). Of the total explained variation, the relative variation explained by the forest cover and fruit diversity variables varied across species (Fig.14).

In species-specific response to the different predictors, I found a positive association between forest cover in a 300 m radius around the transect and the presence of the Mountain Imperial-pigeon (Tjur $R^2 = 0.15$) and Malabar Gray Hornbill (Tjur $R^2 = 0.07$) (Fig. 15). The presence of the open-forest Red-whiskered Bulbul (Tjur $R^2 = 0.299$) was negatively associated with forest cover (300 m) (Fig. 15). I found a positive association between the presence of the Great Hornbill (Tjur $R^2 = 0.11$) and Square-tailed Bulbul (Tjur $R^2 = 0.194$) with forest cover in a 1500 m radius around the transect. I found a positive association between the presence of Malabar Gray Hornbill (Tjur $R^2 = 0.07$), White-cheeked Barbet (Tjur $R^2 = 0.066$) and Yellow-browed Bulbul (Tjur $R^2 = 0.10$) and richness of fruiting plants. The presence of Square-tailed Bulbul (Tjur $R^2 = 0.194$) was positively associated with fruit availability. The predictor variables did not explain much variation in the traits ($R^2 = 0.07$). I also did not detect any phylogenetic signal in species niches as the 95% credible interval overlapped zero (posterior mean $\rho = 0.37$ (95% credible interval 0.00–0.93)).

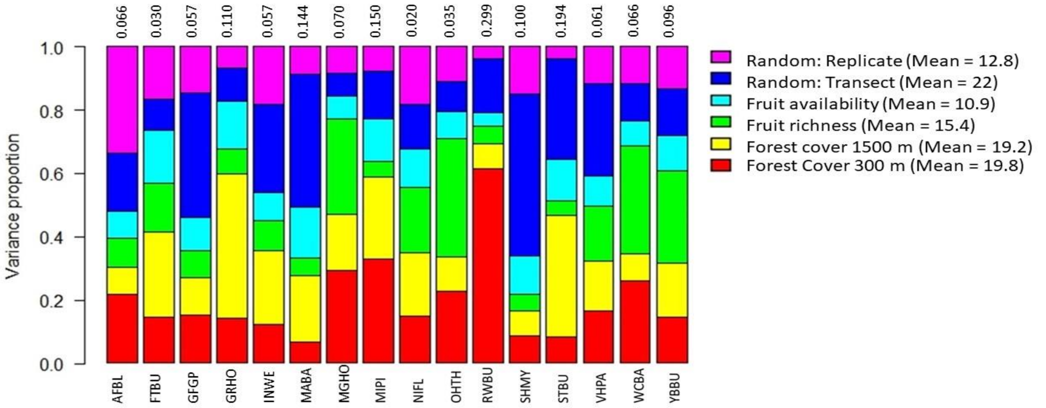

Figure 14. Variance partitioning of fixed and random effects. Figure showing percent of variation explained by different variables. Values above each bar is the Tjur R^2 values (total explained variation) for the respective frugivore. AFBL - Asian Fairy Bluebird, FTBU - Flame-throated Bulbul, GFGP – Gray-fronted Green-Pigeon, INWE - Indian White-eye, MABA - Malabar Barbet, MGHO - Malabar Gray Hornbill, MIPI - Mountain Imperial-Pigeon, NIFL - Nilgiri Flowerpecker, OHTH – Orange-headed Thrush, RWBU – Red-whiskered Bulbul, SHMY - Southern Hill Myna, STBU – Square-tailed Bulbul, VHPA- Vernal Hanging Parrot, WCBA - White-cheeked Barbet, YBBU - Yellow-browed Bulbul.

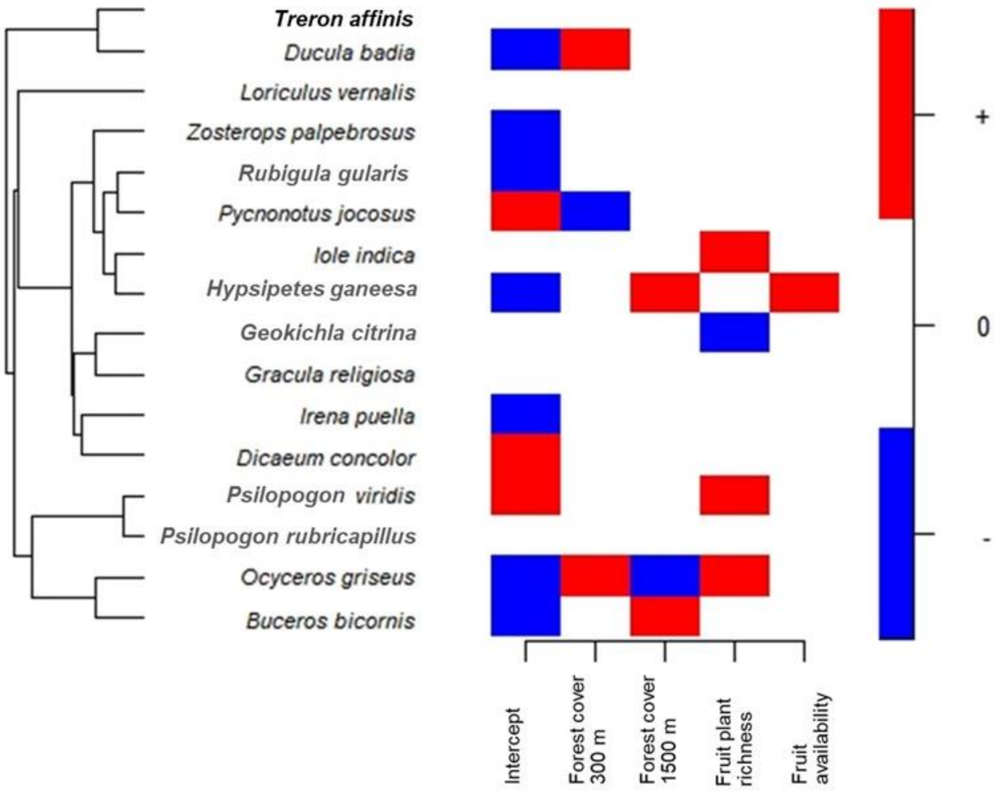

Figure 15. Plot of beta parameter (response of species to the covariates). Species are in rows and predictors are in columns. Red/blue boxes indicate that 95% credible intervals for the beta-coefficients did not overlap zero. Red boxes indicate positive coefficient values and blue boxes indicate negative coefficient values.

DISCUSSION

In this study, I highlight the functional value of small fragments in the Valparai landscape and highlight the critical functional value of *Ficus* and the large-bodied Malabar Gray Hornbill in the landscape. As per my expectations, I found that the fruit availability of small-seeded plant species decreased with increasing forest cover (at 1500 m scale) and fruit availability of medium-seeded plant species increased with increasing forest cover (at 1500 m scale). The presence of certain large-bodied frugivores (and Square-tailed Bulbul) was positively associated with forest cover at different scales. Contrary to my expectations, I did not find any relationship between the large-seeded fruit species and the diversity of frugivores.

Functional value of smaller fragments

This is one of the first studies to systematically quantify the availability of fruit resources in sites across a gradient of forest cover (but see Morante-Filho et al. 2018). Fragmentation negatively impacts large-seeded species (Cramer et al., 2007; Osuri and Sankaran 2016). For large-seeded plants, I failed to find a relationship between the richness and abundance of fruits, and forest cover at both scales (300 m and 1500 m), indicating the prevalence of large-seeded fruits in smaller fragments during the study period. An introduced, large-seeded species *Maesopsis eminii*, which is consumed by hornbills (Pawar et al. 2018), is locally common in the forest fragments. However, the species was not fruiting during the study period. Thus, these results are not influenced by the availability of introduced fruits. Interestingly, I found that the availability (but not richness) of medium-seeded fruits increased with forest cover (1500 m scale), however, the explained variation was low. Interestingly, the availability and diversity of small-seeded plants decreased with forest cover. Unlike the medium-seeded plants, the explained variation in small-seeded fruit availability by forest cover was higher. The greater prevalence of small-seeded species characterizes smaller fragments due to a combination of factors, including edge effects and greater habitat degradation (Jain et al. 2021), which likely influences the availability of small fruits. While I suspected that open-forest and/or invasive species (e.g. *Villebrunnea*, *Lantana*) might influence the fruit availability of small-seeded plants. Preliminary exploratory analysis (not presented here) indicates that variation in fig fruit availability influences this pattern is unlikely to be influenced by open-forest or invasive species ($r < 0.1$). *Ficus* can have large fruit crop sizes, and they can disproportionately influence these patterns. While I found a reduced availability of fruits of certain *Ficus* species with forest cover, there were other *Ficus* species for which the availability increased ($r > 0.2$). The relative contribution of different fruiting plant species to decreased fruit availability needs to be explored in greater detail in future. However, the prevalence of diversity and abundance of fruits even in smaller fragments highlights the functional value of fragments to frugivores. Though the smaller fragments might not encompass home ranges of larger frugivores like hornbills that are known to range over several square kilometers (Naniwadekar et al., 2019b), they might still serve as ‘oases’ offering fruit resources in the larger human-modified landscape.

Fragmentation is known to negatively influence the diversity of forest specialists and large-bodied frugivores (Kirika et al., 2008; Farwig et al., 2017; Bonfim et al., 2021; Jain et al., 2021). In the study area as well, Great Hornbills and other frugivores are thought to be influenced by fragmentation (Raman & Mudappa, 2003; Gopal et al., 2020). Given this background, I had expected to find a positive relationship between frugivore diversity and forest cover (habitat amount). However, I failed to find a relationship between frugivore diversity and forest cover. This highlights the value of the small fragments in the landscape in harbouring frugivore diversity. For example, even the larger-bodied Malabar Gray Hornbill is known to breed in the smallest fragments highlighting the role of these fragments for frugivores for foraging (and nesting) (Fig. 16).

Figure 16. Malabar Gray Hornbill male at its nest in one of the smallest fragments that was sampled. Malabar Gray Hornbill was identified as a key frugivore in the landscape. Photograph: R. Naniwadekar/Wikimedia Commons.

Frugivore responses to fragmentation and resource availability

Frugivores are known to track fruit resources at different scales (Garcia et al., 2004; Naniwadekar et al., 2015). I simultaneously examined the influence of forest cover and fruit resource availability for the different frugivore species found in the landscape and found that different frugivores track different kinds of resources (forest cover and fruit resource availability). Interestingly, the three of the top five key frugivores in the landscape (Malabar Gray Hornbill, White-cheeked Barbet and Yellow-browed Bulbul), as identified by this study, track fruit richness. A previous study has reported a positive relationship between fruit species richness and the abundance of Malabar Gray Hornbill (Raman and Mudappa, 2004). Interestingly, we found a positive relationship between Malabar Gray Hornbill presence and forest cover at the 300 m buffer radius. While Malabar Gray Hornbills are known to persist in the landscape, its population is declining, especially in the plantations (Pawar et al., 2021). Malabar Gray Hornbill is a critical frugivore for this landscape, as identified by this study, and it has been reported to persist even in fragments. The declines in hornbill abundance highlights the need for a long-term study to identify the drivers of population declines. For an inexplicable reason, I found a negative relationship between forest cover at the scale of 1500 m and Malabar Gray Hornbill, which needs to be explored in greater detail in the future.

Two other large-bodied frugivores, Great Hornbill and Mountain Imperial-Pigeon, also exhibited positive relationships with habitat amount. These birds range over large areas explaining the positive relationship with habitat amount (McConkey et al., 2004; Naniwadekar et al., 2019b). Given the energy expenditure on ranging over large distances, especially in these human-modified landscapes, they can be expected to prefer larger patches of forests that are more likely to harbor a greater quantity of fruit resources due to the extent of habitat. Interestingly, the Square-tailed Bulbul, which is a small-bodied frugivore but is known to migrate seasonally (Naniwadekar et al. unpublished data), and occurs in large flocks, tracked forest cover and fruit availability.

Sympatric frugivores track resources at different scales (Naniwadekar et al., 2015; Jayanth, 2020). The sympatric bulbuls in the landscape appear to be exhibiting that trend with the Square-tailed Bulbul tracking fruit availability and larger patches of forest, Yellow-browed Bulbul tracking fruit richness and the Red-whiskered Bulbul tracking open forests. This likely allows the coexistence of closely-related sympatric species and also contributes to the absence of phylogenetic signal in explaining species niches.

Hornbill and the figs

Figs are keystone resources in tropical forests (Shanahan et al., 2001). Even in my study, the top five species in the community were figs. Given that habitat and fruit resources are relatively patchily distributed in these human-modified landscapes, figs are the key resources. Since a single fig tree can bear several orders of fruits than other tree species, they offer a significant quantity of fruits to frugivores. In human-modified landscapes with inhospitable matrix, this can be a critical resource as highlighted by this study. It is important to protect the existing fig trees from anthropogenic pressures and to plant native fig species in the matrix habitat, wherever an opportunity exists. In north-east India, climbers like *Rubus* are the most important members in the community (Jain et al., 2021). It is a likely outcome of the greater degradation of those forests than the fragments in my study area.

In mainland sites, while hornbills are critical dispersers of large-seeded species, they rarely play the most important role in the community (Naniwadekar et al., 2019a; Jain et al., 2021). That role is generally played by the smaller-bodied frugivores like bulbuls, barbets and fairy bluebird (Sankamethawee et al., 2011; Naniwadekar et al., 2019a; Jain et al., 2021). Given the greater diversity of small-seeded plant species and greater abundance of smaller-bodied frugivores in tropical forests, they likely play a more important role in the community. A recent study found that on an island with only seven species of avian frugivores, the largest frugivore, Narcondam Hornbill, played a central role in the community in natural absence of bulbuls and barbets on the island (Naniwadekar et al. 2021). Interestingly, my study found that the larger-bodied Malabar Gray Hornbill played the most important role in the community. While the Malabar Gray Hornbill is large-bodied, it weighs only around 300 g, unlike the largest sympatric hornbill in the landscape, the Great Hornbill, which weighs 4 kg. The smaller body size and yet the larger beak allows it to feed efficiently on small and large fruits, and occur in smaller fragments. Given the immense diversity of other smaller hornbills in Asian tropics across different genera like *Penelopides*, *Anorrhinus*, *Berenicornis* and *Anthracoceros*, determining the ecological role of the smaller hornbills is important. A recent study in tropical fragmented forests in north-east India found that the Brown Hornbill *Anorrhinus austeni* bred in intermediate-sized fragments and played an important role in the removal of large seeds (Jain et al. 2021). More such studies are required to know the role of smaller-sized hornbills.

Limitations of the study

This study only spanned over five months. A long-term study spanning multiple years and a longer duration within a year is needed to determine the consistency of observed trends in this study. I was only able to determine the organisation at the landscape scale and not at the scale of small, medium and large forest patches. Detailed information on the organisation of plant-seed disperser communities across different fragment size classes will be insightful. The marginal R^2 values for the mixed-models, and explained variation for many species in Joint Species Distribution Modelling was low, highlighting the need to document a greater number of variables in the future (e.g. habitat features - tree density, basal area, understorey cover). The outcome of anthropogenic impacts on plants is vital to understand. Despite the alterations in the frugivore community due to anthropogenic threats, the outcomes may remain unaltered (Farwig et al., 2017). While I planned to determine visitation rates of frugivores for a diverse array of frugivores across different fragment size classes, I failed to complete that due to restrictions imposed by the second COVID-19 wave. Valparai landscape is a special case. The human-modified plateau is surrounded by large contiguous patches of forests that are well protected. This is generally not the case in other places. My failure to find otherwise reported trends in the literature (e.g. decrease in frugivore richness with decreasing forest cover) could be because of spillover effects from the adjacent forests. More studies are required in other fragmented forests in the Western Ghats to determine the relationship between forest cover and frugivore richness and abundance.

Despite the shortcomings, the study contributes novel information. By focusing on the entire community of plants and seed dispersers, this study complemented a previous study that focused on four plant species at the study site (Gopal et al., 2020). Most information on the impacts of fragmentation on plant-frugivore communities is from the Neotropics (Emer et al., 2018; Marjakangas et al., 2020). There is very little information from the Asian tropics (Jain et al., 2021). This study builds on Jain et al., (2021) by sampling a higher number of fragments across a wide gradient of fragment size and focusing on forest cover (habitat amount) instead of fragment size. This is also one of the first studies to estimate the availability of fruits across different seed size classes and demonstrates that small fragments harbor a similar set of fruits per unit area as large fragments. This study unequivocally demonstrates the functional role of small fragments, figs and hornbills in human-modified landscapes in Asian tropics, highlighting the need to conserve and restore every remnant patch of forest in the hyperdiverse Asian tropics.

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APPENDICES

Appendix 1. List of fruiting plant species observed during study period

Scientific name	**Seed size**	**Habit**	**Family**
Actinodaphne malabarica	medium	tree	Lauraceae
Aporosa indoacuminata	medium	shrub	Euphorbiaceae
Ardisia pauciflora	small	shrub	Primulaceae
Bhesa indica	large	tree	Celastraceae
Bischofia javanica	small	tree	Euphorbiaceae
Bridelia scandens	small	climber	Phyllanthaceae
Canarium strictum	large	tree	Burseraceae
Sarcandra chloranthoides	small	shrub	Chloranthaceae
Clerodendrum viscosum	small	shrub	Verbenaceae
Coffea arabica	medium	shrub	Rubiaceae
Cryptocarya wightiana	medium	tree	Lauraceae
Cullenia exarillata	large	tree	Bombacaceae
Dendrocnide sinuata	small	shrub	Urticaceae
Dysoxylum binectariferum	large	tree	Meliaceae
Elaeocarpus munronii	medium	tree	Elaeocarpaceae
Erythropalum scandens	medium	climber	Erythropalaceae
Euodia lunu-ankenda	small	tree	Rutaceae
Ficus amplissima	small	tree	Moraceae
Ficus exasperata	small	tree	Moraceae
Ficus microcarpa	small	tree	Moraceae
Ficus nervosa	small	tree	Moraceae
Ficus sp1	small	climber	Moraceae
Ficus sp2	small	tree	Moraceae
Ficus tinctoria	small	tree	Moraceae
Ficus tsjahela	small	tree	Moraceae
Glochidion ellipticum	small	tree	Euphorbiaceae
Gomphandra coriacea	medium	tree	Icacinaceae

Heynea trijuga	medium	tree	Meliaceae
Lantana_camara	small	shrub	Verbenaceae
Leea indica	small	shrub	Leeaceae
Ligustrum perrottetii	small	tree	Oleaceae
Litsea oleoides	large	tree	Lauraceae
Litsea stocksii	medium	tree	Lauraceae
Macaranga indica	small	tree	Euphorbiaceae
Macaranga peltata	small	tree	Euphorbiaceae
Maesopsis eminii	large	tree	Rhamnaceae
Myristica dactyloides	large	tree	Myristicaceae
Persea macrantha	medium	tree	Lauraceae
Psycotria sp	small	shrub	Rubiaceae
Rubus ellipticus	small	climber	Rosaceae
Rubus sp	small	climber	Rosaceae
Sarcocca sp	small	shrub	Buxaceae
Sarcostigma kleinii	large	climber	Icacinaceae
Semecarpus travancorica	large	tree	Anacardiaceae
Symplocos sp	small	shrub	Symplocaceae
Syzigium sp	medium	tree	Myrtaceae
Toddalia asiatica	medium	climber	Rutaceae
Villebrunea integrifolia	small	tree	Urticaceae

Appendix 2. List of plant species involved in interactions.

Species code	**Scientific name**	**Seed size**	**Habit**	**Family**
acma	*Actinodaphne malabarica*	medium	tree	Lauraceae
bija	*Bischofia javanica*	small	tree	Euphorbiaceae
arhe	*Artocarpus hytrophyllus*	large	tree	Moraceae
sach	*Sarcandra chloranthoides*	small	shrub	Chloranthaceae
clvi	*Clerodendrum viscosum*	small	shrub	Verbenaceae
coar	*Coffea arabica*	medium	shrub	Rubiaceae
crwi	*Cryptocarya wightiana*	medium	tree	Lauraceae
elmu	*Elaeocarpus munronii*	medium	tree	Elaeocarpaceae
ersc	*Erythropalum scandens*	medium	climber	Erythropalaceae
fiam	*Ficus amplissima*	small	tree	Moraceae
fiex	*Ficus exasperata*	small	tree	Moraceae
fide	*Filicium decipiens*	small	tree	Sapindaceae
fisp1	*Ficus* sp1	small	tree	Moraceae
fisp2	*Ficus* sp2	small	tree	Moraceae
fiti	*Ficus tinctoria*	small	tree	Moraceae
fits	*Ficus tsjahela*	small	tree	Moraceae
glel	*Glochidion ellipticum*	small	tree	Euphorbiaceae
hetr	*Heynea trijuga*	medium	tree	Meliaceae
laca	*Lantana camara*	small	shrub	Verbenaceae
liol	*Litsea oleoides*	large	tree	Lauraceae
main	*Macaranga indica*	small	tree	Euphorbiaceae
pema	*Persea macrantha*	medium	tree	Lauraceae
pssp	*Psycotria* sp	small	shrub	Rubiaceae
ruel	*Rubus ellipticus*	small	climber	Rosaceae
rusp1	*Rubus* sp	small	climber	Rosaceae
sakl	*Sarcostigma kleinii*	large	climber	Icacinaceae
setr	*Semecarpus travancorica*	large	tree	Anacardiaceae
sysp	*Symplocos* sp	small	shrub	Symplocaceae

viin	*Villebrunea integrifolia*	small	tree	Urticaceae
fire	*Ficus religiosa*	small	tree	Moraceae
fivi	*Ficus virens*	small	tree	Moraceae
flmo	*Flacourtia montana*	small	tree	Flacourtiaceae
knat	*Knema attenuata*	large	tree	Myristicaceae
mein	*Maesa indica*	small	shrub	Primulaceae
losp	*Loranthus* sp	small	parasite	Loranthaceae

Appendix 3. Bird and mammal species seen feeding on fruit during study period.

Species code	**Scientific name**	**Common name**	**Family**
Birds			
afbl	*Irena puella*	Asian Fairy Bluebird	Irenidae
bhcu	*Coracina melanoptera*	Black-headed Cuckooshrike	Campephagidae
ftbu	*Rubigula gularis*	Flame-throated Bulbul	Pycnonotidae
gfgp	*Treron affinis*	Gray-fronted Green-Pigeon	Columbidae
grho	*Buceros bicornis*	Great Hornbill	Bucerotidae
inwe	*Zosterops palpebrosus*	Indian White-eye	Zosteropidae
maba	*Psilopogon rubricapillus*	Malabar Barbet	Megalaimidae
mgho	*Ocyceros griseus*	Malabar Gray Hornbill	Bucerotidae
mipi	*Ducula badia*	Mountain Imperial-Pigeon	Columbidae
nifl	*Dicaeum concolor*	Nilgiri Flowerpecker	Dicaeidae
ohth	*Geokichla citrina*	Orange-headed Thrush	Turdidae
rwbu	*Pycnonotus jocosus*	Red-whiskered Bulbul	Pycnonotidae
shmy	*Gracula religiosa*	Southern Hill Myna	Sturnidae
stbu	*Hypsipetes ganeesa*	Square-tailed Bulbul	Pycnonotidae
vhpa	*Loriculus vernalis*	Vernal Hanging-parrot	Psittacidae
wcba	*Psilopogon viridis*	White-cheeked Barbet	Megalaimidae
ybbu	*Iole indica*	Yellow-browed Bulbul	Pycnonotidae
Mammals			
boma	*Macaca radiata*	Bonnnet Macaque	Cercopithecidae
mgsq	*Ratufa indica*	Malabar Giant Squirrel	Sciuridae
nila	*Trachypithecus johnii*	Nilgiri Langur	Cercopithecidae