

Forest cover and fruit crop size differentially influence frugivory of select rainforest tree species in Western Ghats, India

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Abstract

Forest fragmentation and habitat loss are major disruptors of plant–frugivore interactions, affecting seed dispersal and altering recruitment patterns of the dependent tree species. In a heterogeneous production landscape (primarily tea and coffee plantations) in the southern Western Ghats, India, we examined effects of surrounding forest cover and fruit crop size on frugivory of four rainforest bird-dispersed tree species ($N = 131$ trees, ≥ 30 trees per species, observed for 623 hr). Frugivore composition differed among the four tree species with the large-seeded *Canarium strictum* and *Myristica dactyloides* being exclusively dependent on large-bodied avian frugivores, whereas medium-seeded *Persea macrantha* and *Heynea trijuga* were predominantly visited by small-bodied and large-bodied avian frugivores, respectively. Using the seed-dispersal-effectiveness framework, we identified effective frugivores and examined their responses to forest cover and fruit crop size. Results were idiosyncratic and were governed by plant and frugivore traits. Visitations to medium-seeded *Persea* had a positive relationship with forest cover but the relationship was negative for the large-seeded *Myristica*. In addition, two of the three effective frugivores for *Persea* responded to the interactive effect of forest cover and fruit crop size. Frugivore visitations to *Heynea* were not related to forest cover or fruit crop, and there were too few visitations to *Canarium* to discern any trends. These results highlight the context-specific responses of plant–frugivore interactions to forest cover and fruit crop size influenced by plant and frugivore traits.

KEYWORDS

forest cover, fragmentation, frugivory, fruit crop, seed size, Western Ghats

1 | INTRODUCTION

In the tropics, where more than 75% of plants rely on vertebrates for seed dispersal (Howe & Smallwood, 1982), frugivores play an important role in maintaining plant community structure and diversity (Terborgh, Pitman, Silman, Schichter, & Núñez, 2002).

Forest fragmentation and habitat loss are major factors affecting plant–frugivore interactions (McConkey et al., 2012; Newbold et al., 2013). By altering the plant community composition and reducing fruiting resources, forest fragmentation alters frugivore communities, which may lead to altered recruitment patterns of dependent trees (Cordeiro & Howe, 2003; Cramer, Mesquita, &

Williamson, 2007; Naniwadekar, Shukla, Isvaran, & Datta, 2015; Wotton & Kelly, 2011). Effects of fragmentation on plant–frugivore interactions are non-random and are mediated by “response traits”—such as body size and dispersal ability of frugivores, and seed size of plants—which are most susceptible to habitat disturbance (Hagen et al., 2012; Luck & Daily, 2003). For example, frugivore gape-size limitation constrains large-seeded plants to be dependent on a small set of large-bodied frugivores, which are often the first to be lost following fragmentation and habitat loss (Bregman, Sekercioglu, & Tobias, 2014; McConkey et al., 2012; Newbold et al., 2013). In contrast, small-seeded plants are relatively resilient to fragmentation as they are dispersed by a larger set of frugivores (Farwig, Böhning-Gaese, & Bleher, 2006; Menke, Böhning-Gaese, & Schleuning, 2012; Neuschulz, Botzat, & Farwig, 2011). However, exceptions to these patterns exist. For example, the large-bodied Trumpeter Hornbill (*Bycanistes bucinator*) in South Africa not only persists in a fragmented landscape but also moves long distances between forest patches providing functional connectivity between patches (Lenz et al., 2011). Similarly, some small-seeded species, such as *Ficus thonningii* and *Celtis durandii*, are also likely to be affected due to fragmentation and local disturbance (Kirika, Bleher, Böhning-Gaese, Chira, & Farwig, 2008; Kirika, Farwig, & Böhning-Gaese, 2008).

Frugivores track fruit resources at various spatial and temporal scales, and their movements are governed by fruit availability and forest cover in the landscape (Carlo, García, Martínez, Gleditsch, & Morales, 2013; García & Ortiz-Pulido, 2004; García, Zamora, & Amico, 2011; Naniwadekar, Mishra, & Datta, 2015), which can be important drivers of frugivore visitations to fruiting trees (Blendinger & Villegas, 2011; Martínez & García, 2015). While some studies have shown that neighborhood effects play a role in governing frugivore visitations to focal trees (Blendinger, Loiselle, & Blake, 2008; Saracco, Collazo, Groom, & Carlo, 2005; Smith & McWilliams, 2014), other studies have shown that frugivore visitations are governed by the crop size of the focal tree (Blendinger & Villegas, 2011; Naniwadekar, Mishra, et al., 2015; Ramaswami, Santharam, & Quader, 2019). In addition, frugivore visitations can be potentially governed by the neighborhood effects independent of forest cover (Albrecht, Neuschulz, & Farwig, 2012). Forest fragmentation and the resulting changes in spatial configuration of forest patches and fruiting resources are likely to affect the movement of frugivores and, hence, their visitations to focal trees (González-Varo, Carvalho, Arroyo, & Jordano, 2017; Herrera & García, 2010; Herrera, Morales, & García, 2011; Lehouck et al., 2009). Thus, it is the interaction of the frugivore community (post-filtration of vulnerable traits due to fragmentation) with forest cover and fruit crop size that can be expected to govern visitation trends to the focal trees.

Frugivores vary in their roles as dispersers, and their overall effectiveness for a dependent plant species is governed by quantitative and qualitative components (Schupp, 1993). The quantitative component is determined by the number of seeds dispersed, whereas likelihood of survival of dispersed seeds until the recruitment stage determines the qualitative component (Schupp, 1993; Schupp,

Jordano, & Gómez, 2010). As such, certain frugivores (frugivores with high quantitative and qualitative components) play a crucial role as dispersers and their loss is likely to have a much more pronounced negative effect on dependent plant species (Schleuning, Fründ, & García, 2015). Using the seed-dispersal-effectiveness (SDE) framework (Schupp et al., 2010), we identified effective frugivores for four tree species (two large-seeded species and two medium-seeded species) and examined how the visitation rates of these frugivores varied along a gradient of forest cover around the focal tree and with respect to fruit crop size. Specifically, we examined whether reduction in surrounding forest cover (a) resulted in reduced visitations by effective frugivores to the focal trees and (b) affected large-seeded tree species more than medium-seeded species.

2 | METHODS

2.1 | Study area

The study was conducted on the Valparai Plateau (220 km², 10°15′–10°22′N, 76°52′–76°59′E) and in the adjoining Anamalai Tiger Reserve (958 km², 10°12′–10°35′N, 76°49′–77°24′E) in the southern Western Ghats, India (Figure 1). The Valparai Plateau has an undulating terrain ranging from 600 to 1,500 m above mean sea level. It receives around 3,000 mm of rainfall annually, of which about 70% falls during the southwest monsoon (June to September). The natural vegetation is classified as mid-elevation tropical wet evergreen forests of the *Cullenia exarillata*–*Mesua ferrea*–*Palaquium ellipticum* type (Pascal, Ramesh, & Franceschi, 2004).

The plateau is dominated by plantations of tea (112.4 km², 51% of the plateau) and shade coffee (25.02 km², 11% of the plateau) with small areas of cardamom, and *Eucalyptus* plantations (Mudappa & Raman, 2007). These plantations, especially shade coffee, retain large native trees such as *Persea macrantha*, *Heynea trijuga*, *Myristica dactyloides*, *Canarium strictum*, and *Ficus* spp. in addition to non-native trees such as *Maesopsis eminii* and *Grevillea robusta*. These resources in the matrix are not only exploited as food resources but are also used for nesting by large-bodied frugivores such as hornbills, highlighting the potential resource availability in these habitats (Pawar, Naniwadekar, Raman, & Mudappa, 2018). The plateau has over forty rainforest fragments ranging in size from 1 to 300 ha (in total 10 km², 4.5% of the plateau) which are enmeshed in this production landscape. These fragments are mostly the legacies of the large-scale conversion of the rainforests to plantations from the late 1800s to 1940s (Mudappa & Raman, 2007). The plateau itself is surrounded by relatively undisturbed forests of the Anamalai Tiger Reserve, Parambikulam Tiger Reserve (634 km²), and Vazhachal Reserved Forests (413.95 km²), together comprising a large contiguous protected forest (Figure 1). The tropical wet evergreen forests of the Anamalai Tiger Reserve are also used by forest-dwelling Kadar, Muthuvar, and Malai Malasar tribal people from a few small villages in the reserve, who also gather *Myristica dactyloides* (nutmeg and mace) and resin (black dammar) from *Canarium strictum* for subsistence use

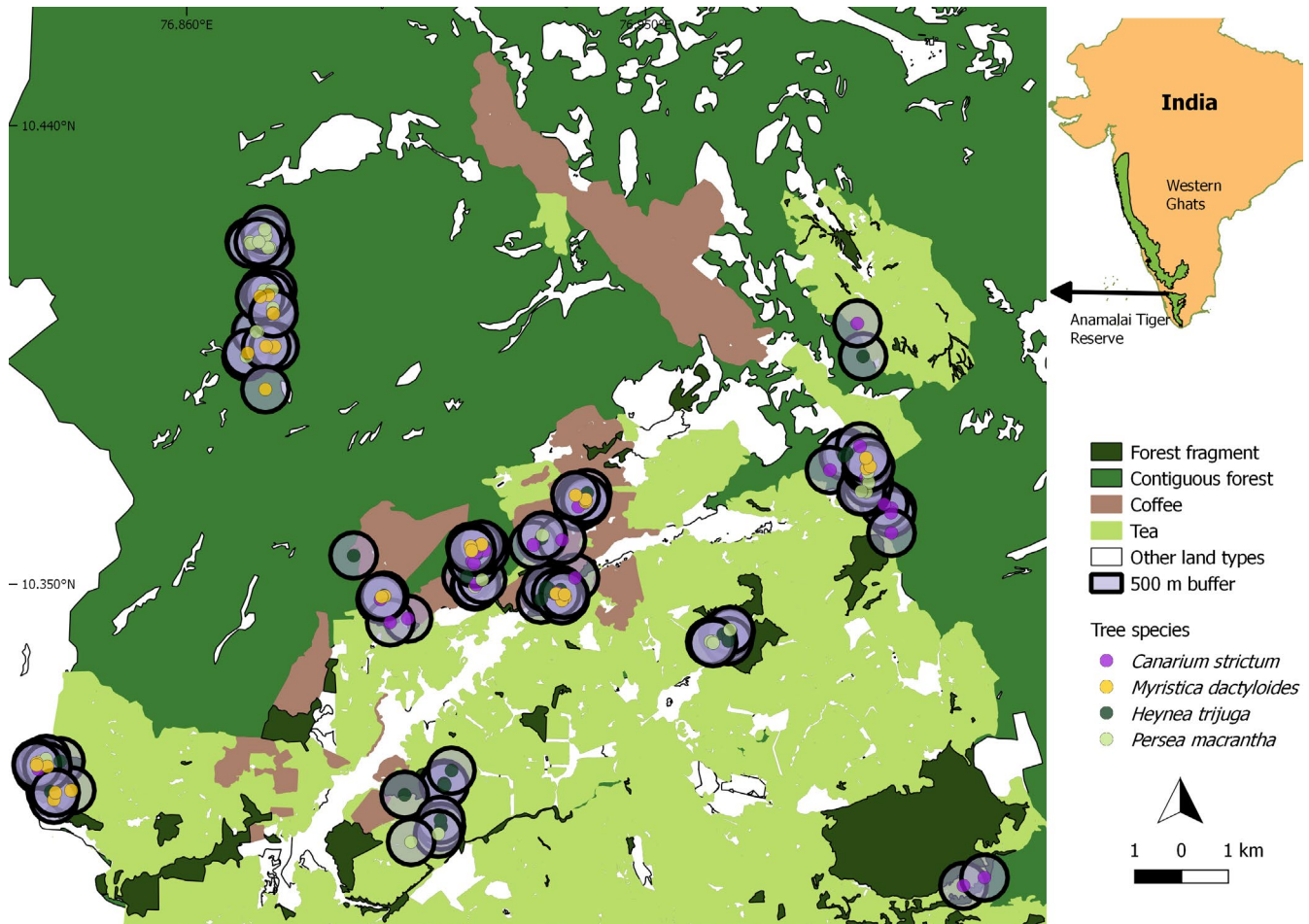


FIGURE 1 The map of the Valparai Plateau and the adjoining forest of the Anamalai Tiger Reserve. The map shows the location of the focal trees and the habitat types they are located in. Circular dots represent individual trees of tree species, and the circles around the points indicate 500 m buffers. The classified maps of the Plateau and the surrounding forest were taken from Wordley, Sankaran, Mudappa, and Altringham (2015)

and sale (Chandi, 2008). The study was conducted from November 2017 to May 2018, which in this landscape represents a period of fruiting resource scarcity to fruiting resource abundance.

2.2 | Study species

Trees were classified as medium-seeded (seed width ≤ 1.5 cm and seed length > 1 cm and ≤ 3 cm) or large-seeded (seed width ≥ 1.5 cm and seed length ≥ 3 cm), following Naniwadekar, Chaplod, Datta, Rathore, and Sridhar (2019), where seeds greater than 1.5 cm in width were predominantly swallowed by large-bodied frugivores (≥ 0.1 kg). Four bird-dispersed tree species (Osuri et al., 2017), two medium-seeded species, *Persea macrantha* (Lauraceae, mean seed width \pm SE = 1.25 ± 0.01 cm, mean seed length \pm SE = 0.93 ± 0.01 cm, $N = 139$) and *Heynea trijuga* (Meliaceae, mean seed width = 1.30 ± 0.01 cm, mean seed length = 1.19 ± 0.01 cm, $N = 113$), and two large-seeded species *Myristica dactyloides* (Myristicaceae, mean seed width = 2.38 ± 0.01 cm, mean seed length = 3.69 ± 0.04 cm,

$N = 109$) and *Canarium strictum* (Burseraceae, mean seed width = 1.82 ± 0.02 cm, mean seed length = 4.02 ± 0.04 cm, $N = 110$), hereafter referred to by their respective genera, were selected for study (refer to Table S1 for more details). The selection was based on their fruiting phenophase during the study period (Nature Conservation Foundation (NCF)—Anamalai Restoration Programme (ARP) unpubl. data), and their relative abundance which enabled the selection of an adequate number of sample trees (Muthuramkumar et al., 2006, Table 1). *Persea* is a canopy tree, with peak fruiting season from March to April (NCF-ARP unpubl. data). The fruits are single-seeded globose drupes (Gamble & Fischer, 1915–1935: 2:1227; Ramesh et al., 2010). *Heynea* is a mid-story tree often found in the edges and in the opening of evergreen to semi-evergreen forests. The seeds are covered by a fleshy white aril (Gamble & Fischer, 1915–1935: 1:183; Ramesh et al., 2010), with the peak fruiting season from December to January (NCF-ARP unpubl. data). *Myristica* is a mid-story tree with peak fruiting season from March to May (NCF-ARP unpubl. data). The fruits are a dehiscent capsule with an arillate seed (Gamble & Fischer, 1915–1935: 3:1214; Ramesh et al., 2010). *Canarium* is an

TABLE 1 Summary details of the observed tree species, sampling effort, and frugivore visitations. *Persea macrantha* and *Heynea trijuga* are medium-seeded, and *Myristica dactyloides* and *Canarium strictum* are large-seeded tree species

Tree species (N = number of trees observed)	Observed duration (hr)	Median fruit crop size (range)	Focal trees with frugivore visitors	Frugivore species seen	Total visits	Mean frugivore visitation rate per hour (SE)
<i>Persea macrantha</i> (N = 32)	149.62	69 (5–600)	32	18	2,400	16.38 (0.04)
<i>Heynea trijuga</i> (N = 36)	173.85	323.5 (20–1900)	21	8	251	1.53 (0.04)
<i>Myristica dactyloides</i> (N = 33)	154.55	5 (1–44)	24	3	126	0.74 (0.04)
<i>Canarium strictum</i> (N = 30)	144.8	290 (30–1200)	6	1	13	0.07 (0.05)
Total (N = 131)	622.82	—	83	18	2,790	—

emergent tree, with a very long fruiting season from August to January (NCF-ARP unpubl. data). The fruit is a large, fleshy drupe with a three-seeded stone (Gamble & Fischer, 1915–1935:1:172; Ramesh et al., 2010). *Heynea* and *Canarium* fruit during a general fruiting scarcity in the landscape, whereas *Persea* and *Myristica* fruit when the overall availability of fruiting starts to increase in the landscape (NCF-ARP unpubl. data).

2.3 | Fruit tree watches

At least thirty individual trees per species were selected for tree watches across a gradient of forest cover (Table 1). Fruiting trees were selected using a combination of field surveys and prior knowledge of existing trees in the landscape. These selected trees were not randomly distributed but were selected based on logistics and their distribution in relation to whether they were in low or high forest cover (Figure 1). To ensure independence at the scale of fruiting trees, focal trees were separated from each other by a distance of at least 30 m. Fruit tree watches were carried out to determine the number of frugivore species visiting the focal tree, their visitation rates, and their fruit handling behavior. Focal trees were watched for a minimum of five hours in the morning (starting from 06:00 to 07:30 hr) and for a minimum of four hours in the afternoon (starting from 12:00 to 13:30 hr). The average duration of observation was 5.6 (± 0.3 SD) hr in the morning and 4.3 (± 0.53 SD) h in the afternoon. The sunrise and sunset in the winter (November–January) and in the summer (February–May) were around 06:40 hr and 18:00 hr, and 06:00 hr and 18:30 hr, respectively. Each tree was observed in a single sampling bout, either in the morning or in the afternoon. In total, 131 individual trees were watched for a total observation period of 623 hr (Table 1). Observations on the focal trees were made using binoculars (Nikon 10 × 50 and Nikon 10 × 42) from a distance of 10–30 m and from a hide if there was no natural cover. Two observers watched the tree, one noting the arrival and the departure times of the frugivores and the other doing focal observations on an individual frugivore, to record its handling behavior, until it left the tree or until it was no longer visible in the canopy. In the case of more than one frugivore species, the rarer species were prioritized for focal observations. During the focal observations, the following events were recorded for the fruit handling: (a) pecked, (b) swallowed, (c) dropped, (d) regurgitated, and (e) removed (events where the birds removed the

fruit and flew away). Fruit crop was estimated at the end of the tree watch by counting the number of ripe fruits in the visible part of the canopy and then extrapolating it to the entire canopy (Table 1; Davidar & Morton, 1986). Only the ripe fruits in the case of drupaceous fruits (*Canarium* and *Persea*) and the dehiscent fruits in the case of capsular fruits (*Myristica* and *Heynea*) were considered for the analysis.

2.4 | Analysis

Fruit crop size and the proportion of forest cover around the focal tree were used as predictors to examine their influence on the visitation rates of frugivores. Since fragmentation is characterized as a landscape-level consequence of breaking up of and loss of habitat (Fahrig, 2003), the proportion of forest cover in a radius of 500 m (0.79 km²) around the focal tree was used as a proxy to look at effects of forest fragmentation following Farwig, Schabo, and Albrecht (2017) (Figure 1). Fruit crop was \log_{10} -transformed to scale the extreme values. Collinearity was checked for the covariates for each tree species using Spearman's rank correlation test. While previous studies have found a positive effect of fruiting neighborhood on frugivore visitations (e.g., Blendinger et al., 2008; Saracco et al., 2005), studies have also found no effect of fruiting neighborhood on frugivore visitations (e.g., Ramaswami et al., 2019). In addition, these studies examined effect of neighborhood at relatively small spatial scales of 30 m around the fruiting tree. As such, the influence of fruiting neighborhood on frugivore visitation patterns was not examined in this study since most frugivores range over large areas (Naniwadekar, Rathore, Shukla, Chaplod, & Datta, 2019; Ramaswami, Kaushik, Prasad, Sukumar, & Westcott, 2016), which preclude the establishment of large plots around focal fruiting trees due to topography and dense vegetation.

2.5 | Seed-dispersal-effectiveness landscape (SDE landscape)

The SDE landscape was constructed with mean visitation rates of frugivore species on the x-axis and the proportion of fruits swallowed on the y-axis to identify effective frugivores, following Schupp et al. (2010) and Jordano (2014). The responses, in terms of

visitation rates, of these effective frugivores to forest cover and fruit crop were examined per tree species. The analysis was not carried out for *Canarium* due to very few frugivore visits (Table 1). Visitation rates were used instead of fruits swallowed per visit as the majority of the data on the fruit handling had incomplete focal samples as it was difficult to observe the frugivores for the entire duration of their stay in the focal tree. Frugivores that had the highest overall effectiveness were considered as effective frugivores. However, only those frugivores for which the data on the proportion of fruit swallowed could be obtained and which visited $\geq 35\%$ of the total trees (approximately one-third of the tree watches) observed were considered for the further GLM analysis.

2.6 | Visitation rate of effective frugivores

To examine the influence of forest cover and fruit crop size on frugivore visitations, a generalized linear model (GLM) with negative binomial error structure was used (as the Poisson model showed over-dispersion) for *Persea* and *Myristica*, except in the case of Malabar Grey Hornbill (*Ocyrceros griseus*) visiting *Persea*, where we used GLM with Poisson error structure. For *Heynea*, negative binomial a GLM with a zero-inflated error structure was used as the data were zero-inflated. The offset function, which is the log-transformed observation effort per tree (in hours), was used to control for variable observation duration across the different trees. Five candidate models with two predictor variables (forest cover and \log_{10} fruit crop size) and an intercept-only model were defined following Johnson and Omland (2004). The different models were ranked using the Akaike information criterion, and models with $\Delta AIC_c < 2$ were considered to be strongly supported by the data (Burnham & Anderson, 2002). In case of model uncertainty, model averaging of all the candidate models (models with cumulative weight ≤ 0.95) was done using a subset or a conditional average (Grueber, Nakagawa, Laws, & Jamieson, 2011), and 95% beta-coefficients of each covariate was computed. Coefficients for which the 95% confidence interval (CI) did not overlap zero were interpreted to influence the response variable. Model averaging was done using R package MuMIn (Ver. 1.42.1, Barton, 2019). In the case of *Myristica*, the top model was bootstrapped to check for the influence of the outlier, but the coefficients did not overlap zero. All analyses were carried out in R 3.5.2 (R Core Team, 2018).

3 | RESULTS

Overall, 2,790 visits by 18 frugivore species (Tables S2 and S3) were recorded for the four tree species in 623 hr of observation (Table 1). The medium-seeded *Persea* had more than ten times the visitation rate per hour as compared to *Heynea* (Table 1). For the large-seeded species, *Myristica* and *Canarium*, the visitation rates were less than one per hour and only six out of the thirty *Canarium* trees observed had visitors (Table 1). The large-seeded species were exclusively

dependent on large-bodied frugivores such as the hornbills and Mountain Imperial-Pigeon (*Ducula badia*). Medium-seeded species had both small- and large-bodied dispersers, with *Heynea* being primarily (89% of the total 251 visits) visited by large-bodied frugivores such as the Southern Hill Myna (*Gracula indica*), Mountain Imperial-Pigeon, and Malabar Grey Hornbill, while *Persea* was predominantly visited by small-bodied frugivores such as the Yellow-browed Bulbul (*Iole indica*), Red-whiskered Bulbul (*Pycnonotus jocosus*), and White-cheeked Barbet (*Megalaima viridis*). The most frequent visitor to *Persea* was the Yellow-browed Bulbul (33% of the total 2,400 visits) and to *Heynea* was the Southern Hill Myna (80%, of the total 251 visits) (Table S2). For *Myristica*, the Malabar Grey Hornbill was the most frequent visitor (85%, of the total 126 visits), while *Canarium* was visited by only the Mountain Imperial-Pigeon during the observed period (Table S2).

3.1 | Seed-dispersal-effectiveness landscape

In the seed-dispersal-effectiveness landscape for *Persea*, the Yellow-browed Bulbul had the highest overall effectiveness followed by the White-cheeked Barbet and the Southern Hill Myna (Figure 2a). Although the Red-whiskered Bulbul had a high visitation rate, it was a poor fruit handler (Figure 2a). The large-bodied frugivores (such as the Mountain Imperial-Pigeon and Malabar Grey Hornbill) had low visitations on *Persea* but swallowed a higher proportion of fruits that they handled (Figure 2a). In the case of *Heynea*, the Southern Hill Myna was the most effective frugivore followed by the Malabar Grey Hornbill and White-cheeked Barbet (Figure 2b). Despite having similar seed size as *Persea*, *Heynea* had a less diverse assemblage of frugivores (Figure 2b). The visitations to *Myristica* were made by only three large-bodied frugivores, with the Malabar Grey Hornbill and Great Hornbill (*Buceros bicornis*) being effectively similar, given the higher visitation rate by the former but better fruit handling by the latter species (Figure 2c). However, there were very few visits by the Great Hornbill (Table S2).

For *Persea*, we selected Yellow-browed Bulbul, White-cheeked Barbet, Southern Hill Myna, Red-whiskered Bulbul, and Malabar Grey Hornbill as the effective frugivores, as these had the highest overall effectiveness and together contributed to up to 83% of the total visitations. For *Heynea*, we selected Southern Hill Myna as it had the highest overall effectiveness and contributed up to 80% of the visitations. In *Myristica*, although Great Hornbill had similar overall effectiveness, we selected Malabar Grey Hornbill for further analysis as it contributed up to 85% of the visitations while Great Hornbill contributed only 0.05% of the total visitation.

3.2 | Visitation rates of the effective frugivores

3.2.1 | *Persea*

Higher visitations of the Yellow-browed Bulbul on *Persea* were associated with an increase in surrounding forest cover, and for a given

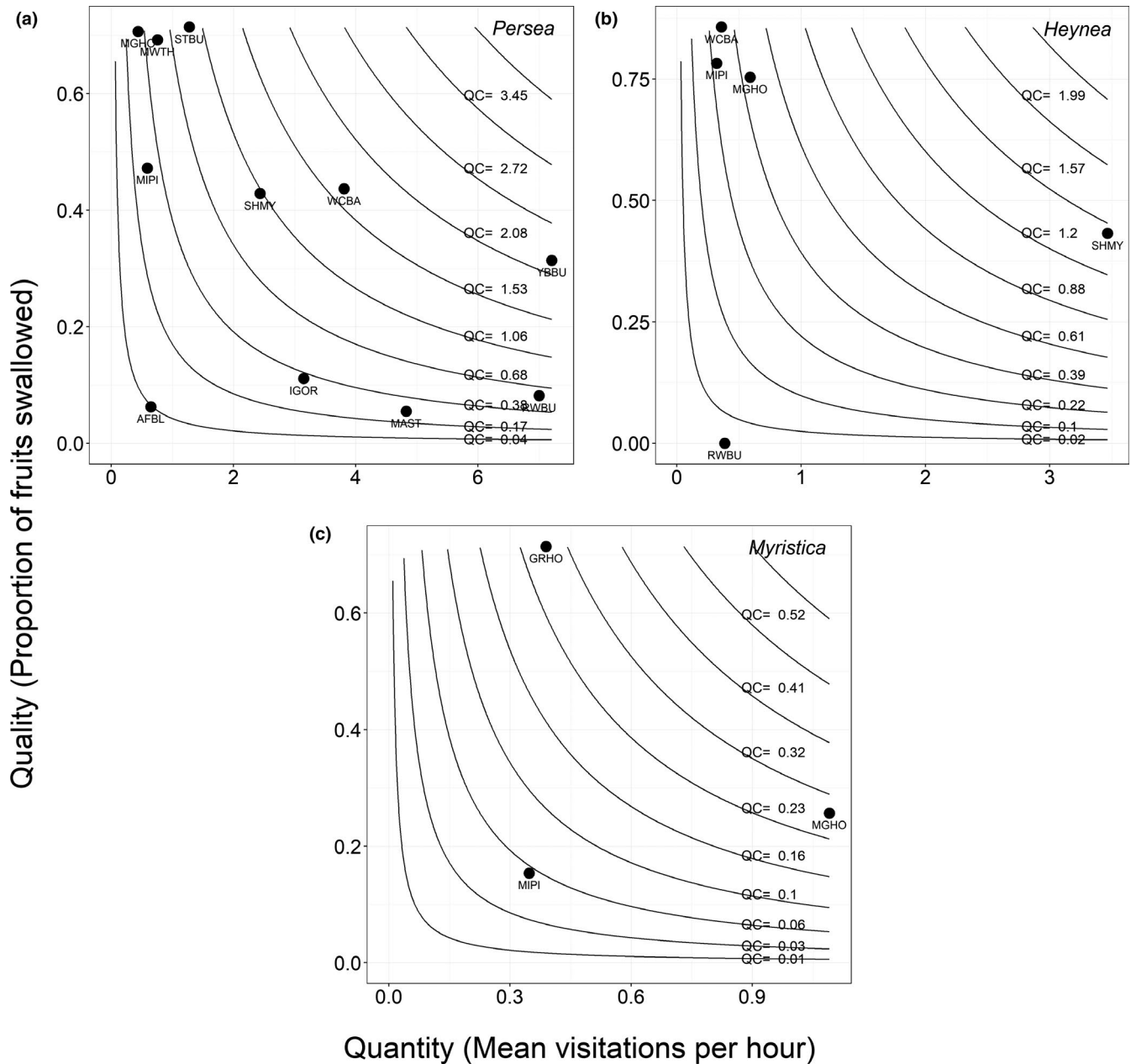


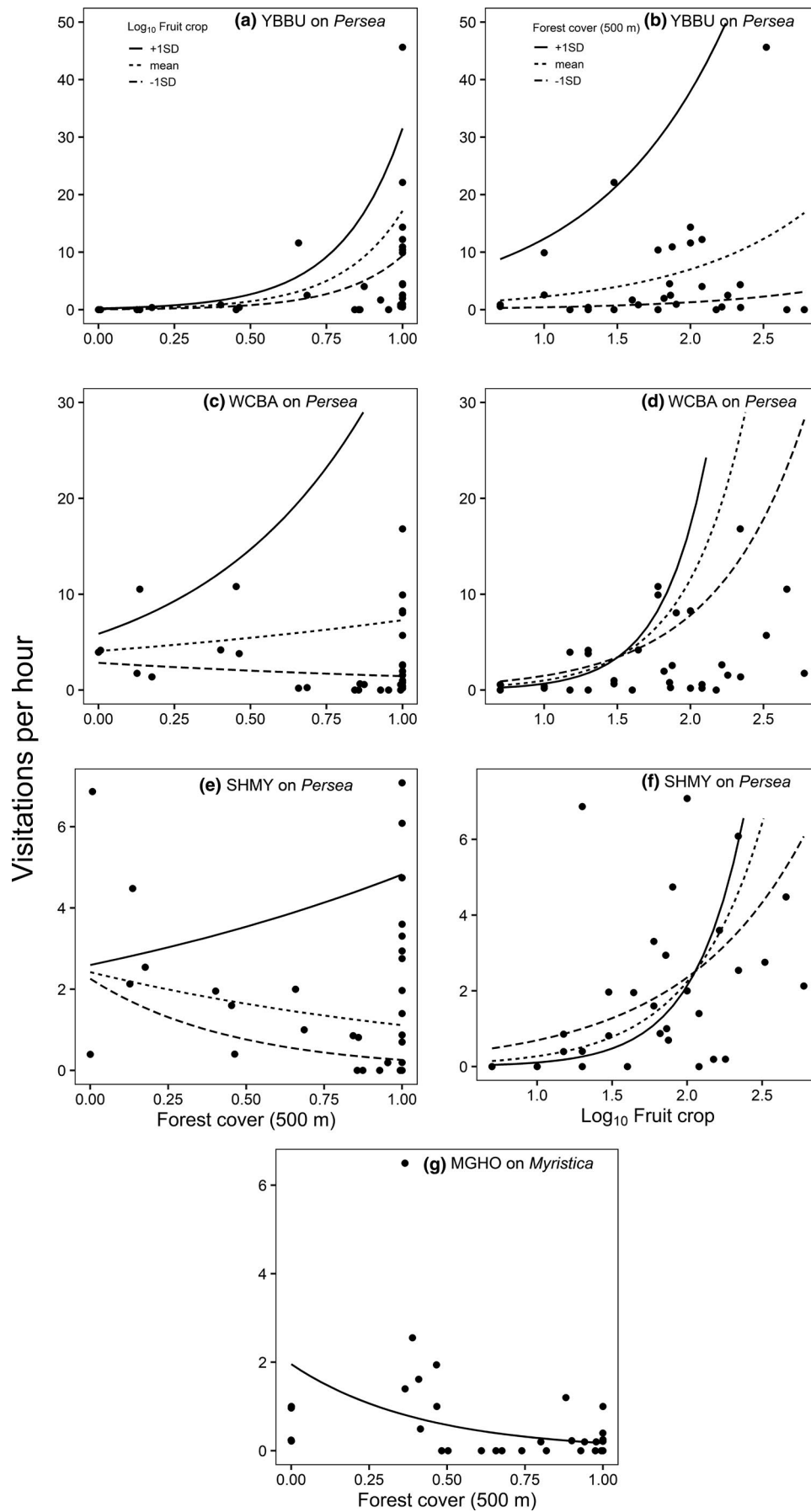
FIGURE 2 The seed disperser effective landscape showing the variation in quantitative component (QC) for (a) *Persea macrantha*, (b) *Heynea trijuga*, and (c) *Myristica dactyloides*. Each point represents the mean visitation rates and the proportion of fruits swallowed by each frugivore species. The isoclines represent all possible combinations of the quantitative and qualitative component that yield the same QC value. For (a) *Persea macrantha*, the frugivores, Yellow-browed Bulbul (YBBU), White-cheeked Barbet (WCBA), and Southern Hill Myna (SHMY) are the most effective dispersers. For (b) *Heynea trijuga*, SHMY is the most effective disperser, whereas for (c) *Myristica dactyloides*, Malabar Grey Hornbill (MGHO) and Great Hornbill (GRHO) are the most effective dispersers. For codes, refer Table S2

forest cover around the focal tree, visitations increased with an increase in fruit crop size (Figure 3a,b). The model with the additive effect between forest cover and fruit crop size had the lowest AIC_c value (Table S4), and the 95% CI for the model-averaged coefficients

for the additive term did not overlap zero (Table 2). The pseudo-*R*² for the top model was 0.40.

For both White-cheeked Barbet and Southern Hill Myna visiting *Persea*, there was a positive relationship with the interaction of forest

FIGURE 3 The relationship of the effective dispersers with forest cover around the focal tree (in a radius of 500 m) and log₁₀ fruit crop size is shown. For *Persea macrantha*, the visitation trend of Yellow-browed Bulbul (YBBU) is driven by the additive effect of forest cover (at the scale of 500 m) and fruit crop size (a, b). For White-cheeked Barbet (WCBA) and Southern Hill Myna (SHMY), the visitations are governed by the interactive effect of forest cover and fruit crop size (c, d and e, f), with the effects of fruit crop being more pronounced on trees with greater surrounding forest cover. For *Myristica dactyloides*, the visitation trends of Malabar Grey Hornbill (MGHO) are governed by a negative relationship with forest cover (g)



cover and fruit crop size (Figure 3c–f). Trees with high surrounding forest cover and with larger fruit crop size had higher visitations. However, in the case of trees with low fruit crop size, there was a higher visitation to trees with low surrounding forest cover as compared to trees with high surrounding forest cover, especially in the case of Southern Hill Myna (Figure 3e,f; minimal change in White-cheeked Barbet). The model with the interaction term between forest cover and fruit crop size had the lowest AIC_C value (Table S4), and the 95% CI for the model-averaged coefficients for the interaction term did not overlap zero (Table 2). The pseudo-*R*² for the top model for both White-cheeked Barbet and the Southern Hill Myna was 0.26 and 0.32, respectively.

For Red-whiskered Bulbul and Malabar Grey Hornbill visiting *Persea*, the top model was within 2ΔAIC_C of the intercept-only model in the case of the Red-whiskered Bulbul and the top model was the intercept-only model in the case of the Malabar Grey Hornbill (Table S4).

3.2.2 | *Heynea*

Of the 36 focal trees, the Southern Hill Myna, despite being the most effective frugivore for *Heynea*, visited only 13 trees with surrounding forest cover ranging from 0.4 to 0.8. Although the model with forest cover had the lowest AIC_C value (Table S4), the 95% CI for the model-averaged coefficients overlapped zero (Table 2).

3.2.3 | *Myristica*

Malabar Grey Hornbill visitations to *Myristica* showed a negative relationship with forest cover, with trees having low surrounding forest cover having higher visitations as compared to trees with high surrounding forest cover. The model with only forest cover had the lowest AIC_C value (Table S4), and the 95% CI for the model-averaged coefficients did not overlap zero (Table 2). The pseudo-*R*² for the top model was 0.20.

TABLE 2 Model-averaged (conditional average) coefficients (for models with cumulative weight ≤0.95) and the associated 95% lower and upper confidence limit (LCL & UCL) for the different parameters are shown. The parameters examining influence of forest cover (in a radius of 500 m from the focal tree) and fruit crop size (log₁₀) on the visitation rates of the frugivores were estimated using generalized linear models with negative binomial error structure in the case of *Persea macrantha* and *Myristica dactyloides*, and zero-inflated negative binomial error structure in the case of *Heynea trijuga*. Parameter coefficients whose 95% CI do not overlap zero have been highlighted in bold

Tree species	Frugivore species	Parameter	Coefficient	95% LCL	95% UCL	Pseudo- <i>R</i> ²
<i>Persea macrantha</i>	Yellow-browed Bulbul	Intercept	-4.07	-7.29	-0.85	.40
		Forest cover	4.94	2.99	6.89	
		Log₁₀ Fruit crop	1.12	0.08	2.17	
	White-cheeked Barbet	Intercept	0.22	-3.52	3.96	.26
		Forest cover	-3.50	-8.63	1.63	
		Log ₁₀ Fruit crop	0.67	-1.22	2.57	
		Forest cover × Log₁₀ Fruit crop	2.33	0.18	4.47	
	Southern Hill Myna	Intercept	0.66	-2.76	4.07	.32
		Forest cover	-5.32	-9.15	-1.50	
		Log ₁₀ Fruit crop	0.13	-1.55	1.81	
		Forest cover × Log₁₀ Fruit crop	2.59	0.64	4.54	
<i>Heynea trijuga</i>	Southern Hill Myna	Count (Intercept)	2.01	-2.51	6.54	.06
		Count (Forest cover)	-1.86	-7.89	4.17	
		Count (Log ₁₀ Fruit crop)	-0.89	-2.32	0.53	
		Zero (Intercept)	215.12	-397.60	827.85	
		Zero (Forest cover)	-598.84	-2449.68	1,251.99	
		Zero (Log ₁₀ Fruit crop)	40.46	-84.89	165.81	
<i>Myristica dactyloides</i>	Malabar Grey Hornbill	Intercept	0.68	-1.02	2.37	.20
		Forest cover	-2.66	-4.80	-0.52	
		Log ₁₀ Fruit crop	0.55	-1.59	2.68	
		Forest cover × Log₁₀ Fruit crop	2.27	-1.49	6.03	

4 | DISCUSSION

Using the seed-dispersal-effectiveness framework, we identified effective frugivores for the four rainforest tree species and examined the response of effective frugivores to forest cover and fruit crop size. Contrary to our expectation, we found a positive relationship with forest cover for *Persea* but a negative relationship with forest cover for the large-seeded *Myristica*. Furthermore, in the case of *Persea*, we documented interactive effects between forest cover and fruit crop size for two of the three frugivores, highlighting context specificity in frugivore responses to forest cover and fruit crop size within and across species (no relationship with respect to fruit crop size for *Myristica*). These results illustrate the context-specific nature of the plant-frugivore interactions and their responses, driven by plant and frugivore traits, to fragmentation.

4.1 | Impacts of forest cover

Effects of fragmentation have been shown to be particularly severe for large-seeded species as they are dependent on specialized large-bodied frugivores, which are the first to be lost due to fragmentation (Bregman et al., 2014; McConkey et al., 2012; Newbold et al., 2013). Small-seeded plants, which are dispersed by a more diverse assemblage of frugivores, are relatively robust to effects of fragmentation as the loss of specialist frugivores is often compensated for by more abundant generalist frugivores (Farwig et al., 2006; Menke et al., 2012; Neuschulz et al., 2011). However, large-bodied frugivores in certain landscapes can move across habitats and provide connectivity between forest fragments (Lenz et al., 2011). In addition, certain landscape-matrix characteristics can facilitate connectivity between fragments by providing key resources for the frugivores (Bhagwat, Willis, Birks, & Whittaker, 2008; Luck & Daily, 2003; Watling, Nowakowski, Donnelly, & Orrock, 2011).

Interestingly, large-seeded *Myristica* showed a contrasting pattern to medium-seeded *Persea*. *Myristica* trees with low surrounding forest cover had higher visitations. This is in contrast to the general understanding that large-seeded species, due to their reliance on large-bodied frugivores, are the most vulnerable to fragmentation (Magrach, Laurance, Larrinaga, & Santamaria, 2014; McConkey et al., 2012; Wotton & Kelly, 2011). The results are likely due to a combination of the traits of *Myristica* and its key disperser, Malabar Grey Hornbill, and the characteristics of the matrix. *Myristica* is a large-seeded species with a lipid-rich arillate fruit and is likely to be highly attractive in the resource-poor matrix (Pawar et al., 2018). In addition, Malabar Grey Hornbills are residents even in small fragments, including some that are surrounded by shade-grown coffee (pers. obs.), and successfully breed and forage in the matrix in this landscape. It is also relatively less specialized and forages on the fruits of understory, mid-story, and canopy trees (Mudappa, 2000). As the fragments and the matrix have lower densities of food plants and large-bodied frugivores, like hornbills (Mudappa & Raman, 2009; Muthuramkumar et al., 2006; Raman, 2006; Raman

& Mudappa, 2003; Sidhu, Raman, & Goodale, 2010), the higher visitations on trees with low surrounding forest cover could be primarily due to aggregation of birds on fruiting trees in a resource-scarce landscape.

The results for *Persea* are in contrast to other studies which show that small-seeded species are relatively robust to fragmentation (e.g., Cramer et al., 2007) due to their diverse dispersers and compensation of loss of forest specialist frugivores by generalist frugivores (Farwig et al., 2006; Menke et al., 2012; Neuschulz et al., 2011). Among the three key frugivores, the Yellow-browed Bulbul is quantitatively the most effective frugivore for *Persea*; by being a numerically abundant, forest specialist frugivore (Raman, 2006; Sidhu et al., 2010), it is likely to play an important role in seed dispersal for *Persea* within a forest patch (Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009). While Yellow-browed Bulbul was quantitatively the most effective frugivore, habitat generalists such as the White-cheeked Barbet and Southern Hill Myna had higher mean visitation rates as compared to Yellow-browed Bulbul on trees with low surrounding forest cover (Figure 3). However, the visitation patterns of the White-cheeked Barbet and Southern Hill Myna were influenced by the interactive effects of fruit crop size and forest cover. This indicates that trees with high fruit crop size and in areas with higher forest cover had higher visitations of White-cheeked Barbet and Southern Hill Myna as compared to trees with high fruit crop size but with low forest cover. Unlike Farwig et al. (2006), in the case of *Persea*, specialist frugivore loss may not be compensated by generalist frugivores as has also been reported elsewhere (Cordeiro & Howe, 2003; Kirika, Bleher, et al., 2008).

4.2 | Resource tracking

Frugivores track highly variable fruiting resources (Herrera, 1985), at different spatial and temporal scales (García et al., 2011; Naniwadekar, Mishra, et al., 2015). Forest fragmentation alters the spatial configuration of forest patches and fruiting resources, spatially restricting access to some resources, thereby altering frugivore movements and thus disrupting seed dispersal patterns at the landscape scale (González-Varo et al., 2017; Herrera & García, 2010; Herrera et al., 2011; Lehouck et al., 2009). Frugivores track resources at spatial scales varying from the level of the fruit crop of an individual tree to the landscape level, contingent on the perceptive scale of the frugivores (García et al., 2011). Here, all the three key frugivores of *Persea* showed signatures of resource tracking at the scale of the fruit crop of the individual tree, which has also been reported in several other studies (Blendinger & Villegas, 2011; Naniwadekar, Mishra, et al., 2015; Ramaswami et al., 2019). Apart from forest cover, fruit crop size also governed the visitation patterns of Yellow-browed Bulbul on *Persea*.

For trees with high surrounding forest cover, Southern Hill Myna and White-cheeked Barbet are more likely to visit trees with high fruit crop size as compared to trees with low fruit crop size. Whereas for the trees with low surrounding forest cover, fruit crop is less

likely to cause variation in visitation rates, as frugivores are likely to exploit a scarce resource more efficiently (Herrera & García, 2009). In future, there is a need to examine the influence of neighborhood fruit availability along with fruit crop size on visitation patterns of frugivores across a gradient of forest cover.

4.3 | Context-specific responses

In this study, we found a context-specific response of frugivores both within and across tree species. Among the four tree species, we found that for the two medium-seeded species, arillate *Heynea* had nearly an order of magnitude lower visitation and half the diversity of frugivores that visited drupaceous *Persea*. While among the large-seeded species, we found that the arillate *Myristica* had more than ten times the visitations as compared to the drupaceous *Canarium* in spite of *Canarium* having significantly higher median fruit crop sizes. As all four trees have lipid-rich fruits, these differences in visitation pattern could be due to the fruiting strategy (arillate versus. drupaceous) and/or the overall nutritional content of the fruits produced by these tree species (Levey & Rio, 2001; Schaefer, Schmidt, & Bairlein, 2003; Stiles, 1993). In addition, the time taken to process the seed (ballast load) and the dietary preferences and requirements of the frugivore could potentially drive the observed patterns (García, Carlo, & Martínez, 2016). However, in the case of *Canarium*, the differences may be amplified due to the long ripening period of the fruits of this tree. Lastly, the study was done from a period of general fruiting resource scarcity to one of the fruiting resource abundance. *Heynea* and *Canarium* fruited during periods of scarcity while *Persea* and *Myristica* during periods of resource abundance, with the fruiting of the latter two species coinciding with the post-nesting phase of hornbills and other frugivores (Mudappa, 2000; Pawar et al., 2018). While the overall peak in fruit availability could potentially lead to differences in visitations among the tree species, frugivores track resources at different scales, from the scale of selecting fruits within a fruiting tree to fruit availability at the landscape level (García et al., 2011; Naniwadekar, Mishra, et al., 2015). As such, at least for frugivores that track fruit resources at local or smaller spatial scales, the observed patterns are likely to remain consistent. Similar patterns have also been reported by Garcia et al. (2016) for co-occurring *Crataegus monogyna* and *Ilex aquifolium* in a temperate landscape and by Farwig et al. (2006) and Kirika, Bleher, et al. (2008) for *Prunus africana* and *Ficus thonningii*, respectively, in a tropical landscape, where small differences in traits of trees and frugivores interact with the landscape to create stronger differences in dispersal even for co-occurring tree species.

The results of this study show idiosyncratic and context-specific responses of frugivores to forest cover and fruit crop size. Among the four bird-dispersed trees, two species showed a contrasting response to forest cover, medium-seeded *Persea* had higher visitations while large-seeded *Myristica* had lower visitations with an increase in forest cover, and there were no trends for the others.

Furthermore, for *Persea* two of three frugivores responded to an interaction of forest cover and fruit crop. Thus, it is the interaction of the frugivore and the plant traits (post-filtration of vulnerable traits due to fragmentation) with the distribution of the resources at the landscape scale that are the likely drivers of visitation patterns in this study. However, further studies are needed to examine whether the variation in the visitation rates by the key frugivores is likely to have a downstream consequence on the recruitment patterns of the dependent tree species (e.g., Muñoz, Schaefer, Böhning-Gaese, & Schleuning, 2017). In addition, long-term studies are required to determine the consistency of these patterns across years and their influence on seed dispersal. Plant-frugivore interactions are a challenging system to study as they are highly variable and span large spatial and temporal scales and over long lifespans of trees. Additionally, fragmentation and the nature of the matrix add an additional layer of complexity as they filter out species with vulnerable traits while allowing the persistence of others. This context specificity makes broad generalizations difficult, especially with respect to seed sizes, and highlights the importance of site-specific observational information. This becomes even more relevant given the context of fragmentation where there is a paucity of studies, especially in the south and South-East Asia, which examine the loss or alteration of resource availability and ecosystem services like seed dispersal due to forest fragmentation and habitat loss (Corlett, 2017; McConkey et al., 2012).

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CONFLICT OF INTEREST

We declare no conflicts of interest.

AUTHOR CONTRIBUTION

AG, RN, DM, and TRSR conceived and designed the study. AG collected the data. AG and RN did the analysis with inputs from DM and TRSR. AG wrote the manuscript with inputs from RN, DM, and TRSR.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5x69p8d0r> and <https://doi.org/10.5061/dryad.q2bvq83g4> (Gopal, Mudappa, Raman, & Naniwadekar, 2020; Naniwadekar, Naniwadekar, & Gopal, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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