Title: The critical ecological role of an endemic, large-bodied frugivore on a small tropical island

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ABSTRACT

Mutualistic interactions, like seed dispersal, are important for maintaining plant diversity in tropics. Islands, which have a smaller subset of plants and frugivores, when compared with mainland communities offer an interesting setting to understand the relative role of ecological and evolutionary processes in influencing the interactions between plants and frugivores. In this study, we examined the relative influence of functional traits and phylogenetic relationships on the plant-seed disperser interactions on an island and a mainland site. The island site allowed us to investigate the organization of the plant-seed disperser community in the natural absence of key frugivore groups (bulbuls and barbets) of Asian tropics. The largest frugivore on the island, the point endemic Narcondam Hornbill, was also the most abundant frugivore on the island and played a significant quantitative and central role in the plant-seed disperser community. Species strength of frugivores was positively associated with frugivore abundance. Among plants, figs had the highest species strength and played a central role in the community during the study period. We found that the island had among the highest reported densities of hornbills and figs in the world. Island-mainland comparison revealed that the island plant-seed disperser community was more asymmetric, connected and nested as compared to the mainland community with which it shared certain plant and frugivore species. Neither functional traits nor phylogenetic relationships were able to explain the patterns of interactions between plants and frugivores on the island or the mainland. Diffused nature of interactions between plants and frugivores, trait convergence and plasticity in foraging behavior likely contribute to shaping the interactions between plants and frugivores. This study underscores the need to study plant-seed disperser communities on tropical islands, particularly in the Indian Ocean, which have inadequate representation in the literature.

Key words: Asian Koel, community phylogenetics, figs (*Ficus*), insular communities, Narcondam Hornbill, Pakke, plant-frugivore interactions, seed dispersal

INTRODUCTION

Endozoochory, which is a mutualistic interaction between plants and frugivorous animals, is a critical stage in plant regeneration and contributes to the maintenance of tree diversity in tropics (Terborgh et al. 2002). The community of food plants and seed dispersers form a network of bipartite interactions. These networks could be influenced by different ecological (e.g. functional traits, phenological overlap) and evolutionary (e.g. co-evolution) processes (Vázquez et al. 2009; Guimarães Jr et al. 2011). There are limited studies that have investigated the relative role of eco-evolutionary processes on plant-seed disperser interactions.

Interactions could be influenced by trait complementarity which could be modulated by trait conservatism or trait convergence (Rezende et al. 2007; Bastazini et al. 2017). Trait conservatism will result in closely related species interacting with similar partners. On the other hand, interactions could be influenced by trait convergence wherein a similar trait is exhibited by unrelated species. Interacting communities often exhibit organize themselves into modules. These modules could be organized based on species' shared evolutionary history coupled with similar traits (Donatti et al. 2011) or through trait convergence (Peralta 2016) or abundance (Schleuning et al. 2014*b*). Traits relevant to the seed dispersal services, and the number of partners that a frugivore has, have been demonstrated to exhibit phylogenetic signal (Rezende et al. 2007). Some studies have also detected phylogenetic signal in species that act as connectors between modules that enable network integration (Schleuning et al. 2014*b*). The ecophylogenetic approach outlines four scenarios based on the interactions that are mediated by phylogeny or functional traits, which allows the assessment of relative contribution of traits and phylogenetic relationships on plant-animal interactions (Bastazini et al. 2017). The influence of phylogenetic component would be indicative of the role of evolutionary processes like co-evolution in the

organization of the community, while the influence of functional component controlling for phylogenetic history would imply trait complementarity. This enables an understanding of the relative roles of these factors in community assembly. Despite substantial availability and progress in the use of phylogenetic data in understanding community structure, systematic examination of the role of evolutionary processes in tandem with ecological processes in assembly of plant-frugivore communities is limited.

Bulk of the information on plant-disperser communities are from mainland sites with few studies from oceanic islands and even fewer in an island-mainland comparative framework (Schleuning et al. 2014*a*). Despite zoochory being a pervasive interaction in Asian wet tropics, there is limited information on plant-disperser communities from the mainland Asian wet tropics (Corlett 2017) and very poor information from oceanic islands in the Indian Ocean (Escribano-Avila et al. 2018). Island systems have experienced a disproportionately higher percentage of species extinctions as compared to mainland systems (Heinen et al. 2018). Given the naturally asymmetric nature of plant-frugivore communities on islands (Schleuning et al. 2014*a*), frugivore loss on islands can be expected to have significant cascading impacts on plant communities. Oceanic barrier restricts the species that can colonize and persist on the island. Therefore, they offer a natural laboratory to evaluate the influence of the absence of key mainland frugivore groups on plant-seed disperser interactions. Comparing distribution of interactions on island and mainland can provide insights into the organization of plant-seed disperser communities.

Given this background, we examined the organization of the plant-disperser community on a remote and small tropical island (Narcondam Island) in South Asia using the network and ecophylogenetic approaches (Fig. 1A). The Narcondam island, which is the only place where the

Narcondam Hornbill *Rhyticeros undulatus* is found (Fig. 1B), is characterized by a species-poor frugivore assemblage, enabled us to examine the relative quantitative role of different species in seed dispersal. In the Asian tropics, small-bodied frugivores like bulbuls and barbets are known to play key roles in seed dispersal (Naniwadekar et al. 2019). However, the Narcondam Island does not have any bulbuls and barbets and most of the dominant frugivores on the island are medium- and large-bodied avian frugivores (> 100 g) (Fig. 1C). This offers an interesting system to understand the distribution of interactions in absence of key frugivore group. We compared this island community with a mainland community from north-east India with which it shares several frugivore and plant species. The specific aims of the study were to 1) identify key seed dispersers and plant groups on an oceanic island community by comparing species-level properties (degree, species strength and weighted betweenness) across different species, 2) examine the influence of abundance and morphological traits on species strength of plants and frugivore species, 3) compare the network-level properties (web asymmetry, connectance, specialization and weighted nestedness) of the island community with a mainland community, and 4) examine the influence of phylogenetic and functional component on the distribution of interactions between plants and frugivores on the island and mainland communities. We expected that large-bodied frugivores will not be restricted by morphological constraints and will demonstrate dietary shifts on islands in the absence of small-bodied frugivore. This will alter the organization of the plant-seed disperser community on the island as compared to mainland. These questions scale up from species-level to community-level and across spatial scales from island to mainland. On the temporal axis, we examine the influence of ecological processes on species roles in community and ecological and evolutionary processes on distribution of interactions in the community. This system allowed us to explicitly examine the change in the

role of large-bodied frugivores in plant-seed disperser communities in the absence of small frugivores (Fig. 1C).

MATERIALS AND METHODS

Study area: The study was carried out on a small (area: 6.8 km^2), volcanic island, the Narcondam Island (13º30'N, 94º38'E), in the Andaman Sea in India. The island is part of the Indo-Myanmar Biodiversity Hotspot (Myers et al. 2000). Three distinct vegetation types on the island include the narrow strip of littoral forests, forests dominated by deciduous species in the north-eastern part of the island and evergreen forests in most of the island (Page et al. in prep.).

The Endangered Narcondam Hornbill *Rhyticeros narcondami* is found only on the Narcondam Island (BirdLife International 2017). Around 50 species of birds have been reported from the island (Raman et al. 2013). There are two terrestrial mammals on the island, including a shrew (*Corcidura* sp.) and an invasive rat (*Rattus* sp.). There are at least four species of bats on the island including a fruit bat species (*Pteropus hypomelanus*). Narcondam Hornbill (body mass: 600-750 g) is the largest frugivore on the island. Additional details of study area are in Appendix S1.

Frugivore and plant abundance: We conducted the study between December 2019 – February 2020. We used variable-width line-transect surveys to estimate the density and abundance of birds on Narcondam Island (Thomas et al. 2010). We walked 20 unique trails on the island (Appendix S2: Fig. S1). We divided the entire elevation gradient into three elevation zones: low (0-200 m), mid (200-400 m) and high (400-700 m) based on topography, vegetation structure and composition. One to three observers walked trails in the mornings and afternoons. During

the trail walks, we recorded species identity, the number of individuals and the perpendicular distance of the sighting to the trail. The trail lengths varied between 0.22–1.26 km and the total sampling effort was 51.4 km (Appendix S2: Table S1).

We laid 49 belt transects (50 m × 10 m) across the three different elevation zones (low: 18, mid: 14, high: 17) to estimate the richness and abundance of woody plants on the Narcondam Island. Within the belt, we enumerated all wood plants that were ≥ 10 cm GBH (girth at breast height) along with their girth and taxonomic identity.

Plant-frugivore interactions: To systematically document plant-frugivore interactions, we performed spot-sampling during our trail walks, and opportunistically outside our trail walks following Palacio *et al*. (2016). Whenever we encountered a frugivore on a fruiting tree, we recorded the species identity, number of frugivores, and frugivore foraging behaviour (fruits swallowed, pecked or dropped) to ascertain whether the frugivore was a seed disperser or not. Plant-frugivore interaction information was systematically collected outside trail sampling whenever frugivore was detected on fruiting trees. To determine if we were missing documenting interactions of frugivore species with low detection probability through spot sampling, we systematically observed fruiting trees. We observed 40 fruiting individuals of 12 species following Naniwadekar et al. (2019a) (Appendix 2: Table S2). Additional details of the tree watches are in Appendix S1. We measured widths of at least five fruits each of 23 species of fleshy-fruited plants following Naniwadekar et al. (2019*a*) (Appendix S2: Table S3). Plants were classified as small-seeded (seed width: < 5 mm), medium-seeded (seed width: 5-15 mm) and large-seeded (> 15 mm) following Naniwadekar et al. (2019a) (Appendix S2: Table S3).

Analysis

Frugivore and plant abundance: We estimated densities of perched birds with more than 40 visual detections using the R package 'Distance' (Thomas et al. 2010; Miller et al. 2019). We estimated combined density of two Imperial-pigeon species (Pied Imperial-Pigeon *Ducula bicolor* and Green Imperial-Pigeon *Ducula aenea*), since we had 45 detections overall. Additional details of the analysis are provided in the Appendix S1. We estimated the overall tree density and basal area (m^2 ha^{-1}), and density of 27 species of fleshy-fruited plants that were fruiting during the study period.

Island plant-seed disperser community: We created a matrix of plants and frugivores with the frequency of interactions documented for each plant-frugivore combination through spot sampling. We only considered those animals as seed dispersers which we had seen swallowing the seeds. We didn't consider Alexandrine Parakeet *Psittacula eupatria* in the analysis as we documented the parakeets predating on seeds or feeding on unripe fruits as has also been documented elsewhere (Shanahan et al. 2001). We plotted the interaction accumulation curve using the 'random' method and 1000 permutations as implemented in the R package 'vegan' to determine if we had adequately documented the diversity of unique plant-seed disperser interactions (Oksanen et al. 2019).

To determine the relative roles of species in the organization of plant-seed disperser communities, we examined species-level properties like the degree (number of mutualistic partners), species strength (importance of species from partner's perspective) and weighted betweenness centrality (connector species connecting multiple guides in community) (Bascompte et al. 2006; Mello et al. 2015). We used the R package 'bipartite' for this analysis (Dormann et al. 2008).

We used the general linear model to examine the influence of abundance (estimated using the vegetation plots) and fruit type (small-seeded, figs, medium-seeded and large-seeded) on species strength of the 27 plant species that were fruiting during the study period. During exploratory analysis, we noticed that figs consistently had higher species strength values. Since certain fig groups are known to be keystone species in tropical forests and provide key nutrients (Shanahan et al. 2001), we performed the analysis with figs as a separate category. Species strength was $\log_{10}$ transformed to approximate normality. In the case of frugivores, since there were only seven species and species strength values were not normally distributed, we used Spearman's ρ to examine the correlation between abundance (encounter rate km^{-1}) of frugivores and body mass with species strength. We obtained body mass information from Wilman et al. (2014). To determine if the island plant-seed disperser community was organized into distinct sub-communities, we used the program MODULAR (Marquitti et al. 2014) following Naniwadekar *et al.* (2019). Additional details in Appendix S1.

Comparing the island and the mainland plant-seed disperser communities: To determine the differences in the organization of plant-seed disperser communities between island and mainland, we compared plant-disperser communities between the Narcondam Island with that of Pakke Tiger Reserve in north-east India. Information on plant-seed disperser communities is limited from the Asian tropics. However, there is detailed information on interactions between 48 avian frugivores and 43 plant species is available from Pakke Tiger Reserve in north-east India (Naniwadekar et al. 2019). Pakke is part of the Eastern Himalaya Biodiversity Hotspot. It is about 1500 km straight line distance north from the Narcondam Island. Representative species of all the frugivore genera found on the Narcondam Island are also found in Pakke with species like the Green Imperial-Pigeon, Asian Koel *Eudynamys scolopaceus* and Common Hill Myna

Gracula religiosa being reported from both sites. Several genera of fleshy-fruited plants found on Narcondam Island are also found in Pakke. Unlike the island community which is relatively young, the mainland site is several million years old. We examined network-level properties like web asymmetry, connectance (proportion of realized interactions), specialization (H_2') and nestedness (weighted NODF) and compared it with the mainland site (Pakke). Values of web asymmetry range between -1 to 1 with negative values indicating higher diversity of plant species as compared to animal species and vice versa (Blüthgen et al. 2007). Specialization is a measure of complementary specialization of the entire network with high values indicating that the species are more selective. Weighted NODF is a quantitative measure of nestedness with high values indicating higher nestedness.

Community assembly on island and mainland: To determine the influence of phylogeny and functional traits on plant-frugivore interactions on the mainland and island site, we used the following approach. The plant phylogeny was pruned from the megaphylogeny (Qian and Jin 2016) for both the island and mainland communities individually. This is a time-calibrated phylogeny with largest representation from 98.6% of families and 51.6% of all genera of seed plants. Scientific names of plants were standardized by referring to 'The Plant List' (www.theplantlist.org). However, some species from Pakke and Narcondam were missing from the megaphylogeny. In those cases, we chose the closest species from the Oriental region. When we failed to find a congener, we chose a genus close to the focal genus (Appendix S2: Table S3). We used fruit width and seed size class information for the analysis (Appendix S2: Table S3). In the case of the birds, we referred to the comprehensive and time-calibrated bird phylogeny available at www.birdtree.org (Jetz et al. 2012). We found all the focal species for the two sites in the database except *Pycnonotus flaviventris*, *Chrysocolaptes guttacristatus* and *Sitta*

cinnamoventris. We used congeners from the Oriental region for these species for the analysis (Appendix S2: Table S4). For the frugivores, we used body mass and percentage fruits in the diet of frugivores (degree of frugivory) obtained from Wilman et al. (2014) (Appendix S2: Table S4). We obtained 100 trees from posterior distribution of 10000 trees based on Ericson Sequenced Species backbone phylogeny with 6670 OTUs for seven bird species for Narcondam and 48 species for Pakke found in the network (Jetz et al. 2012). The maximum clade credibility tree was used for further analyses as these trees did not vary substantially in topology and branch lengths. We calculated the phylogenetic distances (pair-wise distances between species using their branch lengths) using 'cophenetic.phylo' in the R package 'ape' (Paradis and Schliep 2018). We used Gower method to estimate pair-wise distances among traits of both plants and frugivores using "vegdist" in the R package 'vegan'. We then followed the novel approach outlined by Bastazini et al. (2017) to determine whether phylogenetic proximity influenced the evolution of species trait and their interactions in the network or whether species traits influence the observed pattern of interactions after removing the potential confounding effect of the phylogeny. We applied this method for Narcondam and Pakke separately. We used the R packages 'SYNCSA' for this analysis (Debastiani and Pillar 2012; Oksanen et al. 2019). We used R (ver. 3.5.3) for all the analysis (R Core Team 2019).

In addition, we assessed the phylogenetic signal separately in trait data for birds and plants in both sites, Narcondam and Pakke. We calculated the Blomberg's *K* for each trait using the R package "phytools" (Blomberg et al. 2003; Revell 2012).

RESULTS

Frugivore and plant abundance: We detected six avian frugivores during the trail walks. We had 207 visual detections of Narcondam Hornbill, 71 detections of Asian Koel, and 45 detections of the two Imperial-Pigeons. We had only two detections each of the Common Hill Myna and Eye-browed Thrush *Turdus obscurus*. Information on detection probability and mean flock size is summarized in Appendix S2: Table S5.

Narcondam Hornbill was the most common frugivore on the island and its abundance (mean (95% CI): 1026 birds (751-1402)) was almost four times that of the Asian Koel (Fig. 2A; Appendix S1: Table S5). The estimated overall mean (95% CI) density of the Narcondam Hornbill was 151 (110-206) birds km^{-2}. The mean densities of the Narcondam Hornbill varied between 101-168 birds km^{-2} across the three elevation zones with the lowest mean densities in the highest elevation band (Fig. 2B) (Appendix S2: Table S5).

The mean (± SE) density and basal area of all the woody plants (≥ 10 cm GBH) was highest in the 0-200 m elevation band (density: 2091.1 ± 124.4 plants ha^{-1}; basal area (m^2 ha^{-1}): 58.3 ± 5.3), followed by 200-400 m elevation band (density: 1505.7 ± 101.1 plants ha^{-1}; basal area (m^2 ha^{-1}): 49.1 ± 3.0) and least in the 400-700 m elevation band (density: 1311.8 ± 82.7 plants ha^{-1}; basal area (m^2 ha^{-1}): 39.2 ± 4.2). However, the mean abundance of the different categories of the frugivore food plant species (figs, small-seeded non-fig plants, medium-seeded plants and large-seeded plants), which were fruiting during the study period, was highest in the high elevation band (400-700 m), followed by middle elevation band and lowest in the low elevation band (0-200 m) (Fig. 2C).

Island plant-seed disperser community: We documented 752 interactions between seven frugivore species and 27 plant species during the spot scans performed on trail walks and opportunistically. We documented all the frugivore species (except Andaman Green Pigeon

Treron chloropterus) previously reported from the island. We documented the migrant Daurian Starling *Agropsar sturninus*, for the first time. During spot scans on trail walks, we documented 262 interactions between six frugivore species and 19 plant species. During opportunistic spot scans, we documented 490 interactions between seven frugivore species and 26 plant species. Narcondam Hornbill was documented feeding on 22 plant species, followed by Asian Koel, which was documented feeding on 16 plant species (Appendix S2: Table S6). Of the 752 interactions, 533 were of the Narcondam Hornbill, 111 were of the Asian Koel, 36 of the Green Imperial-Pigeon, 34 of the Pied Imperial Pigeon, 25 of the Common Hill Myna, 12 of the Eye-browed Thrush and one of the Daurian Starling. Among the 27 plant species, eight species were represented by *Ficus*. We observed 282 interactions on *Ficus rumphii*, 80 on *Ficus glaberrima*, 54 on the small-seeded *Aidia densiflora* and 50 on the large-seeded *Caryota mitis*. We documented 64 unique interactions between plants and frugivores on the island during the study period. The interaction accumulation curve indicated that we had adequately documented interaction diversity (Appendix S2: Fig. S2).

During tree watches, we documented 684 interactions (Narcondam Hornbill: 481, Asian Koel: 167, Pied Imperial-Pigeon: 23, Green Imperial-Pigeon: 7, Eye-browed Thrush: 5, Common Hill Myna: 1), between 11 plant species and six frugivore species. We did not document any interaction during tree watches which we had not documented during the spot scans. For eight of the 11 tree species, we observed greater diversity of frugivores foraging on the particular plant species during spot sampling as compared to tree watches.

Ficus rumphii (among plants) and Narcondam Hornbill (among frugivores) had the highest degree, species strength and weighted betweenness centrality highlighting the central role they played in the community during the study period (Appendix S2: Table S6). General linear model

indicated that the species strength in plants was influenced by plant type (figs and non-fig small-, medium- and large-seeded plants) and not by plant abundance (Adj. R^2 = 0.40, $F_{4,22}$ = 5.322, p = 0.004) (Fig. 3A; Appendix S2: Table S7). *Ficus* were different from other small-seeded plants and had higher species strength values (mean (± SE) = 0.739 (± 0.101), n = 8 species) as compared to small-seeded (mean (± SE) = 0.0816 (± 0.01), n = 9 species), medium-seeded (mean (± SE) = 0.0376 (± 0.01), n = 6 species) and large-seeded plant species (mean (± SE) = 0.0328 (± 0.01); n = 4 species) (Fig. 3A). Among frugivores, species strength was significantly and positively correlated to their abundance (Spearman's ρ = 0.89, p = 0.0123, n = 7 species; Fig. 3B) and not significantly correlated to their body mass (Spearman's ρ = 0.71, p = 0.088, n= 7).

The observed modularity of the island plant-disperser community was 0.33, and it was not significantly different from that obtained through the null models (p = 0.45). The observed community was subdivided into four modules and all the species were consistently allocated to the same modules across the 25 runs (Table S8). One of the four modules comprised of the Narcondam Hornbill and several medium and all the four large-seeded plants including *Endocomia macrocomia*, *Caryota mitis*, *Pycnarrhaena lucida* and *Planchonella longipetiolata* highlighting hornbill's importance for large-seeded plants (Table S8).

Comparing the island and the mainland plant-seed disperser communities: The island network was more asymmetric (-0.588) as compared to the mainland site (0.044). The observed values of connectance and nestedness on Narcondam were almost twice that of the mainland site and specialization (H_2') was almost half that of the mainland site (Table 1). The observed network on Narcondam was less connected and less weighted than the null model predictions but it was more specialized than expected by random (Table 1).

Community assembly on island and mainland: Among woody plants, we detected a strong phylogenetic signal for seed size and fruit width in Pakke Tiger Reserve (seed size: Blomberg's $K = 0.73$, $p = 0.001$; fruit width: Blomberg's $K = 0.43$, $p = 0.005$) and Narcondam (seed size: Blomberg's $K = 1.48$, $p = 0.001$; fruit width: Blomberg's $K = 0.45$, $p = 0.027$). Among frugivores, we detected a phylogenetic signal for the body mass of frugivores in Pakke (Blomberg's K=1.22, $p = 0.012$) and Narcondam Island (Blomberg's $K = 1.28$, $p = 0.043$). We did not detect phylogenetic signal in the percentage of fruits in the diet of the frugivores of Pakke (Blomberg's $K = 0.23$, $p = 0.38$) and Narcondam (Blomberg's $K = 0.90$, $p = 0.08$). We did not find any significant correlation for the four models indicating that neither the functional or the phylogenetic component was able to explain the observed interaction patterns between plants and frugivores in both island and mainland sites (Table 2; Fig. 4).

DISCUSSION

In this study, we demonstrate the role of large-bodied frugivores, especially the endemic Narcondam Hornbill, in contributing disproportionately to seed dispersal in the absence of key small-bodied frugivore groups on the island. Narcondam Hornbill plays a central role in the plant-dispersal community as it is super-abundant, has very high species strength and betweenness centrality values and is critical for the select large-seeded plants fruiting. This study also demonstrates the key role played by figs in the plant-seed disperser community as demonstrated by its very high species strength values as compared to other plant types. In comparison to the mainland community, the island community was more asymmetric, connected, nested and less-specialized. We have documented trait convergence and dietary shifts in frugivores which potentially contribute to the diffused nature of plant-seed disperser interactions.

This also likely contributes to the absence of the role of phylogenetic or functional component in the assembly of plant-seed disperser communities on mainland or the island. This is one of the few studies from oceanic islands of the Indian Ocean and demonstrates how the largest frugivore, which is a point-endemic, plays a critical quantitative role in seed dispersal. This is also one of the few studies that performed a paired comparison between an island and mainland community.

Narcondam for the hornbill and by the hornbill

There is no other place in the world where hornbills are reported to occur in such high densities as on Narcondam Island (151 birds km^{-2}). On Sulawesi, the Knobbed Hornbills *Rhyticeros cassidix* occur in very high densities of up to 84 birds km^{-2} (Kinnaird et al. 1996). In north-east India, Wreathed Hornbill *Rhyticeros undulatus*, a close relative of the Narcondam Hornbill, seasonally occur in densities of up to 68 birds km^{-2} (Naniwadekar and Datta 2013). Our density estimates are similar to densities estimated by previous studies (Raman et al. 2013; Manchi 2017). Reduction in hunting pressures, following the suggestions by Sankaran (2000), may have resulted in the recovery of Narcondam Hornbill population. Among other frugivores, there is limited information on the density of the Asian Koel from other sites, but comparison with existing studies show that Narcondam has very high densities of as compared to other sites (Riley 2001). The mean Imperial-Pigeon densities are slightly lower than those reported from a mainland site in north-east India (Dasgupta and Hilaluddin 2012).

In this study, multiple measures (abundance and different network metrics – species strength, degree, betweenness and modularity) indicate that Narcondam Hornbills are keystone seed dispersers on the island. Generally, as the body mass increases, the abundance of the frugivore

and the frequency of visitation is found to decline (Godínez-Alvarez et al. 2020). Interestingly, the Narcondam Island is unique where the largest frugivore, the Narcondam Hornbill, is also the most abundant frugivore on the island. Abundant species have been reported to influence their partners strongly and Narcondam Hornbill had the highest species strength values highlighting its importance for plants (Vázquez et al. 2007). Larger frugivores, like hornbills, are known to remove more fruits per visit as compared to other smaller frugivores (Naniwadekar et al. 2019). Highest number of interactions of the Narcondam Hornbill coupled with potentially higher fruit removal rates point towards the key quantitative role played by the hornbill on the island. Modularity analysis revealed that the hornbill was the key seed disperser for the large-seeded plants as has been demonstrated in previous studies (Naniwadekar et al. 2019; Gopal et al. 2020). The hornbill was the only frugivore that has high betweenness centrality value pointing towards its vital role as a connector between different guilds within the community. The Narcondam Hornbill was found to be playing a key role in seed dispersal in this asymmetric system. This high reliance on a frugivore and the potentially low redundancy highlights the fragility of the island ecosystem because of strong reliance on a single frugivore.

Narcondam has very high densities of hornbill food plants, which likely explains the high hornbill densities. The overall fig density on Narcondam Island was 27 trees ha^{-1}. The densities of the six fig species which were consumed by frugivores (including hornbills) was 24 trees ha^{-1}. This is very high as compared to other sites in the world where the densities of hemi-epiphytic figs are typically less than one tree ha^{-1} (Harrison 2005). *Ficus* (species consumed by hornbills) density was 2.7 trees ha^{-1} at a site in north-east India (Datta 2001). *Ficus* (overall) densities were 1.4 trees ha^{-1} at a site in the southern Western Ghats (Page and Shanker 2020). *Ficus* densities of up to 10 trees ha^{-1} have been reported in Sulawesi (Kinnaird et al. 1996). Consistently across the

mainland site and the island site, certain species of *Ficus* attracted the highest diversity of frugivores. On the island, *Ficus* represented the top six species in species strength, highlighting the key role they potentially played in the plant-disperser community at least during the study period if not throughout the year. Association between canopy, hemi-epiphytic figs and hornbills has been documented (Harrison et al. 2003). Most dominant fig species during our study on Narcondam Island, which are important hornbill food plants are mostly canopy, hemi-epiphytic figs. Being small-seeded, they often play the pioneering role in attracting frugivores on oceanic islands and accelerating plant colonization on the island (Harrison 2005). Figs and hornbills may have played a critical role in setting up the plant community on the island which needs further investigation.

Based on published literature on hornbill food plants from north-east (Datta 2001; Naniwadekar et al. 2015, 2019) and Thailand (Poonswad et al. 1998; Kanwatanakid-Savini et al. 2009; Chaisuriyanun et al. 2011), we identified at least 35 species of Narcondam Hornbill food plants. Overall density of the 35 hornbill food plant species (GBH ≥ 30 cm) on Narcondam Island is 327 trees ha^{-1}. In Pakke Tiger Reserve, the density of 45 hornbill food plant species was 163 trees ha^{-1} (Datta 2001), highlighting the hyper abundance of hornbill food plants on Narcondam Island. Interestingly, the abundance of food plants is consistently distributed across the entire elevation gradient. The hyper abundance of frugivores and their food plants makes this island a unique ecosystem.

Plant-seed disperser communities on island and mainland

Island communities have been reported to be more asymmetric as compared to mainland systems due to higher immigration rates of plants or human-caused frugivore extinctions on the island

(Schleuning et al. 2014*a*; Nogales et al. 2016). There are no known human-driven extinctions on the Narcondam island. We are unlikely to find additional species of frugivores that can play an important functional role in seed dispersal on the island as our list of frugivores is comparable to the frugivores reported by the previous studies (Raman et al. 2013). We feel that dispersal limitation of frugivores could also be a key factor in the web asymmetry. Andaman and Nicobar archipelago of which Narcondam Island is part of, is an interesting example of this. Bulbuls and barbets, which are the key frugivores on the mainland (Naniwadekar et al. 2019), are absent on the remote and tiny Narcondam Island. Endemic species of bulbuls are found on other islands in the Andaman and Nicobar archipelago, but barbets are absent from the archipelago. Thus, the variation in the dispersal ability of different frugivore groups might also play an important role in contributing towards the web asymmetry on oceanic islands. Among other network properties, higher connectance on islands has been reported elsewhere (González-Castro et al. 2012). Forbidden links are thought to contribute towards lower connectance (Olesen et al. 2011). Additionally, connectance and nestedness are negatively correlated (Rezende et al. 2007). In our case, higher connectance is associated with higher nestedness on the island site as compared to the mainland site. Given that most of the important frugivores on the island are medium (100-500 g) or large-bodied (> 500 g) with ability to handle small and large fruits, it has likely resulted in higher connectance and nestedness.

Organization of plant-seed disperser communities

We detected a phylogenetic signal in bird body mass and seed and fruit traits on the island and the mainland. However, functional and phylogenetic component did not influence the network interactions in the plant-seed disperser communities on the island and mainland. The role of

evolutionary history in shaping local networks of interacting species is thought to be limited (Segar et al. 2020). Unlike the plant-pollinator networks, the seed dispersal networks can be expected to be less specialized and diffused as unrelated species may exhibit trait convergence and forage on similar plant species (Jordano 2000). We found that distantly related groups of frugivores dispersed seeds of a common assemblage of plants, many of which are distantly related to each other. A diverse array of frugivores disperse the super-generalist *Ficus*, and even the large-seeded plants, which otherwise have a smaller disperser assemblage, were predominantly dispersed by distant frugivore clades, like hornbills and *Ducula* pigeons, on the mainland site. Unlike Bastazini et al. (2017), we did not detect signal in the functional component of the plant-seed disperser communities. This is a likely consequence of the absence of trait complementarity among interacting frugivores and plants. While the small-bodied frugivores may not be able to disperse large seeds due to morphological constraints, large-bodied frugivores like hornbills, fed on plants that were large- and small-seeded resulting in lack of trait complementarity.

Another important reason could be the behavioral plasticity shown by frugivorous birds while foraging. In the mainland site, where there are almost 50 frugivore species with a higher preponderance of small-bodied frugivores, we rarely encountered *Ducula* pigeons on figs that attracted more than half of the frugivore species found in the area. On the mainland site, *Ducula* pigeons were mostly observed foraging on medium-seeded and large-seeded plants. On the island, where there are hardly any small frugivores, we mostly saw the *Ducula* pigeons foraging on *Ficus*. This behavior of *Ducula* pigeons feeding on figs on the island but less frequently on the mainland demonstrates phenotypic plasticity in *Ducula* pigeons, likely as a response to lack of competitive interactions, an aspect that has been seldom documented elsewhere. Additionally,

on Narcondam Island, we documented hornbills feeding on *Callicarpa arborea*, a small-seeded species which is mostly dispersed by bulbuls and barbets on the mainland site (Naniwadekar et al. 2019). Asian Koel, which is a rare frugivore in the mainland site, was seen only once feeding on fruit there. However, on the island, it is the second-most important frugivore. It remains to be determined, whether exploitative competition on the mainland site drives larger frugivores to feed on different resources in the mainland forested system. While habitat fragmentation often results in loss of large-bodied frugivores thereby affecting large-seeded plants, it will be interesting to investigate the implications of the absence of small-bodied frugivore on the structuring of plant communities.

Bats are known to play an important role in seed dispersal on oceanic islands (McConkey and Drake 2015). We recorded spat out wads of pulp of three *Ficus* spp., *Balakata*, and *Planchonella*. Direct detections of foraging bats were mostly near our camp on fruiting *Manilkara zapota* (planted), *Terminalia catappa*, *Ficus rumphii* and *Ardisia*. We failed to detect foraging bats during the six night-walks that lasted for at least 90 minutes each. Role of bats in seed dispersal on the island needs to be evaluated in the future.

One may argue about the lack of phenological completeness of the study and its influence on the inferences drawn. The abundances of the frugivores, which is an independent measure used to demonstrate the relative importance of frugivores, is unlikely to change since it is a tiny and remote island in the middle of the Andaman Sea. Narcondam Hornbill is likely to remain the most abundant frugivore on the island year-round and thereby play a key role in seed dispersal throughout the year. Additionally, the frugivore species composition on the island is unlikely to change as previous studies have documented similar assemblage of frugivores. The frugivore data is relatively robust, and we have had a diverse representation of plant families in our study

with varying fruit (figs, drupes and arillate dehiscent capsular fruits) and seed traits thereby capturing the functional diversity in traits of fruits and seeds making the data amenable for ecophylogenetic analysis. Additionally, this is a remote island making it extremely challenging to conduct long bouts of fieldwork, thereby posing challenges to collect long-term data.

Only those plants and animals that are able to cross the oceanic barriers and establish contribute to structuring of communities on islands. Degree of isolation, area and age of islands thereby offers an interesting gradient to understand the relative importance of processes in structuring of communities. As demonstrated in this study, ;arge-bodied frugivores, particularly the Narcondam Hornbill, play a pivotal role on Narcondam Island in the absence of small frugivores on a relatively young and moderately isolated island. Several threatened hornbill species are found on oceanic islands (IUCN 2019). Narcondam Island and its endemic hornbill give insights into the potential role of hornbills, which are among the largest frugivores on islands, in shaping and potentially maintaining the island tree communities by playing a key role as a seed disperser. The ecological role of hornbills and their contribution to mutualism and maintenance of plant species diversity is poorly understood from other oceanic islands. Narcondam Island through the hyper abundance of hornbills and its food plants and the asymmetric nature of the plant-disperser community with heavy reliance on a single frugivore demonstrates the unique ecological and evolutionary setting of oceanic islands. The disproportionate and singular role that species can play on oceanic islands points towards the extreme vulnerability of oceanic islands to any external perturbations. The perturbations can disrupt the delicate and intricate relationships between plants and seed dispersers, with dramatic cascading impacts on the entire community. Unfortunately, studies like this might not be possible in many other oceanic islands that harbor hornbills as they have been already modified extensively due to anthropogenic activities. It is

indeed fortunate that Narcondam Island has been preserved as a Wildlife Sanctuary thereby safeguarding not only a unique hornbill species but also a unique ecosystem.

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and VR; RN wrote the manuscript with inputs from JJ, AG, NP, SG and VR. All authors gave final approval for publication.

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Table 1. Network-level properties (observed and null model values) for the Narcondam Island, and observed values for the mainland site, Pakke Tiger Reserve. Null model values for the mainland site can be found in Naniwadekar et al. (2019a).

	Observed value: Narcondam	**Null mean: Narcondam**	**Null SD: Narcondam**	**Observed value: Mainland**
Connectance	0.339	0.463	0.018	0.154
Specialization (H_2')	0.233	0.144	0.009	0.500
Weighted NODF	45.178	59.76	3.834	24.885

Table 2. Correlation coefficients for the two models that evaluate the influence of the functional (after removing phylogenetic signal) and phylogenetic components on the observed patterns of interactions between plants and frugivores for the mainland site (Pakke Tiger Reserve) and the island site (Narcondam Wildlife Sanctuary). None of the values were significant at $p = 0.05$.

Parameter	ρ **(Mainland)**	ρ **(Island)**
Functional component (after removing phylogenetic signal)	0.04	0.03
Phylogenetic component	0.023	-0.17

FIGURES

Figure 1. Schematic illustrating mainland and island plant and seed-dispersal communities. A map of the South and Southeast Asia showing mainland and island site (a). The island endemic large-bodied frugivore Narcondam Hornbill *Rhyticeros narcondami* on *Caryota mitis* (b). Organization of plant-seed disperser community on mainland and island. Large-bodied frugivores, many of which predominantly feed on large-seeded plants, can exhibit ecological release on the island (in the absence of small frugivores) resulting in dietary shifts. Dietary changes will in turn result in changes in interaction frequencies with corresponding changes in network structure. Painting and sketches by Sartaj Ghuman. Map source: Google Earth.

Figure 2. Abundance of Narcondam Hornbill *Rhyticeros narcondami*, Asian Koel *Eudynamys scolopaceus* and Imperial-Pigeons (Pied Imperial-Pigeon *Ducula bicolor* and Green Imperial-Pigeon *Ducula aenea*) on Narcondam Island (A). Density (km^{-1}) of Narcondam Hornbill on the island and across the three elevation zones on the island (B). Density (ha^{-1}) of 27 species of fleshy-fruited plants that were fruiting across the three elevation zones during the study period (C).

Figure 3. Relationship between species strength (log_{10} transformed in the case of plants) and plant type (A) and frugivore abundance (B). We separated figs and small-seeded plants for they consistently had higher species strength values. Frugivore codes - ASKO: Asian Koel, CHMY: Common Hill Myna, DAST: Daurian Starling, EBTH: Eye-browed Thrush, GIPI: Green Imperial-Pigeon, NAHO: Narcondam Hornbill and PIPI: Pied Imperial-Pigeon.

Figure 4. Seed dispersal interactions in Narcondam Island (A) and the mainland site, Pakke Tiger Reserve (B). Also shown is the pruned phylogeny for the plants and the frugivores and

respective traits for plants (seed size and fruit width) and frugivores (body mass and percentage diet that is comprised of fruits).

Figure 1.

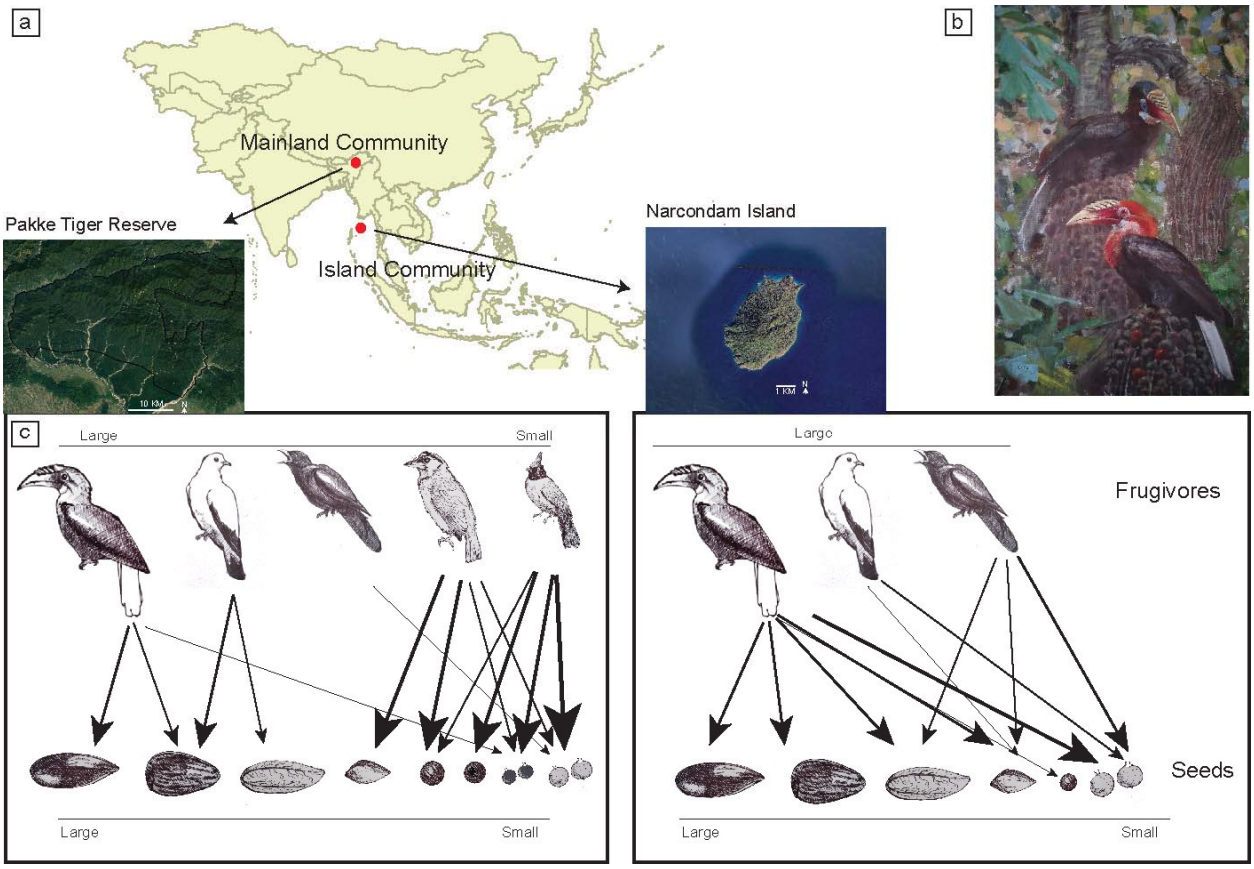

a
Mainland Community
Pakke Tiger Reserve
Island Community
Narcondam Island
b
c
Large
Small
Large
Small
Large
Frugivores
Seeds
Large
Small

Figure 2.

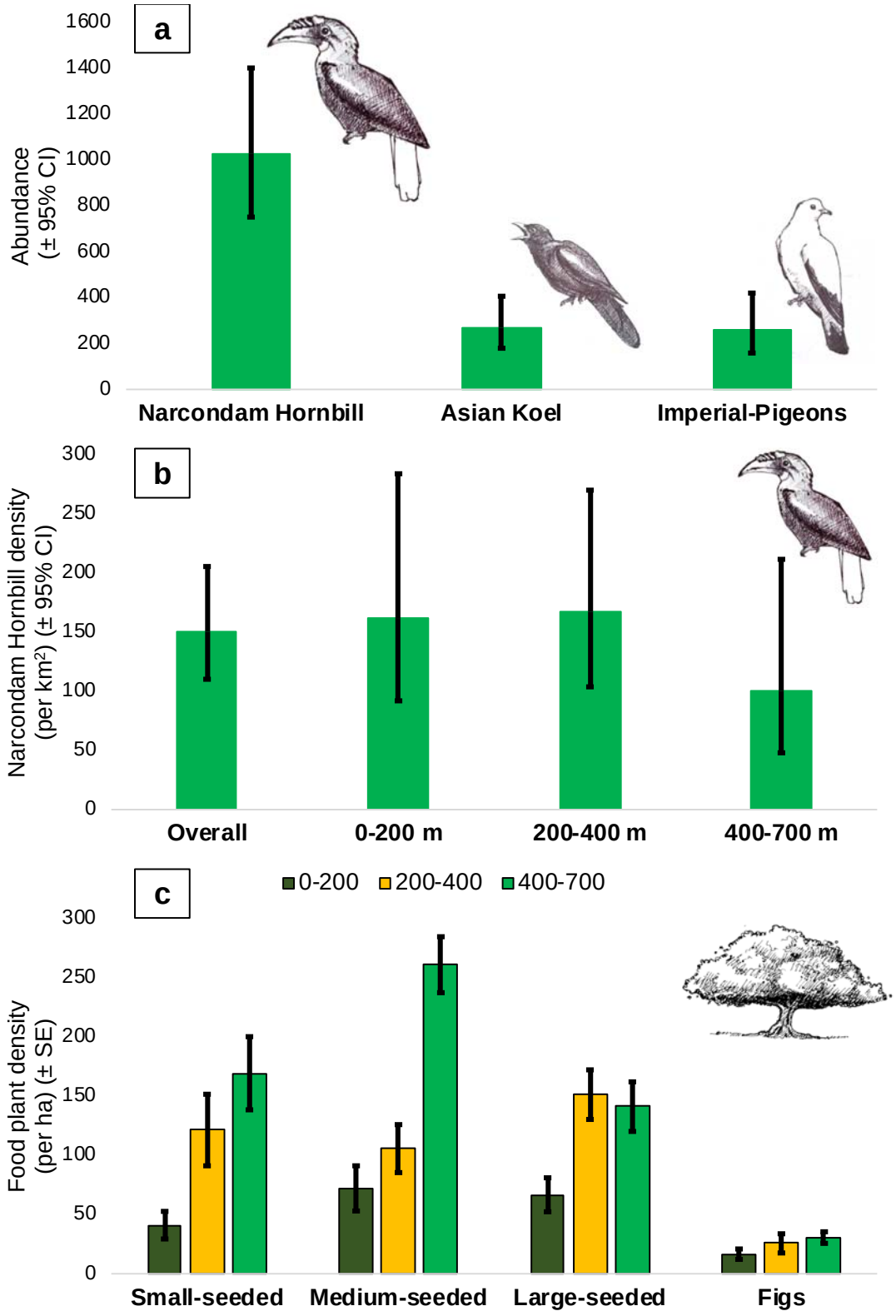

a
Abundance (± 95% CI)
1600
1400
1200
1000
800
600
400
200
0
Narcondam Hornbill
Asian Koel
Imperial-Pigeons
b
Narcondam Hornbill density (per km²) (± 95% CI)
300
250
200
150
100
50
0
Overall
0-200 m
200-400 m
400-700 m
c
0-200
200-400
400-700
Food plant density (per ha) (± SE)
300
250
200
150
100
50
0
Small-seeded
Medium-seeded
Large-seeded
Figs

Figure 3.

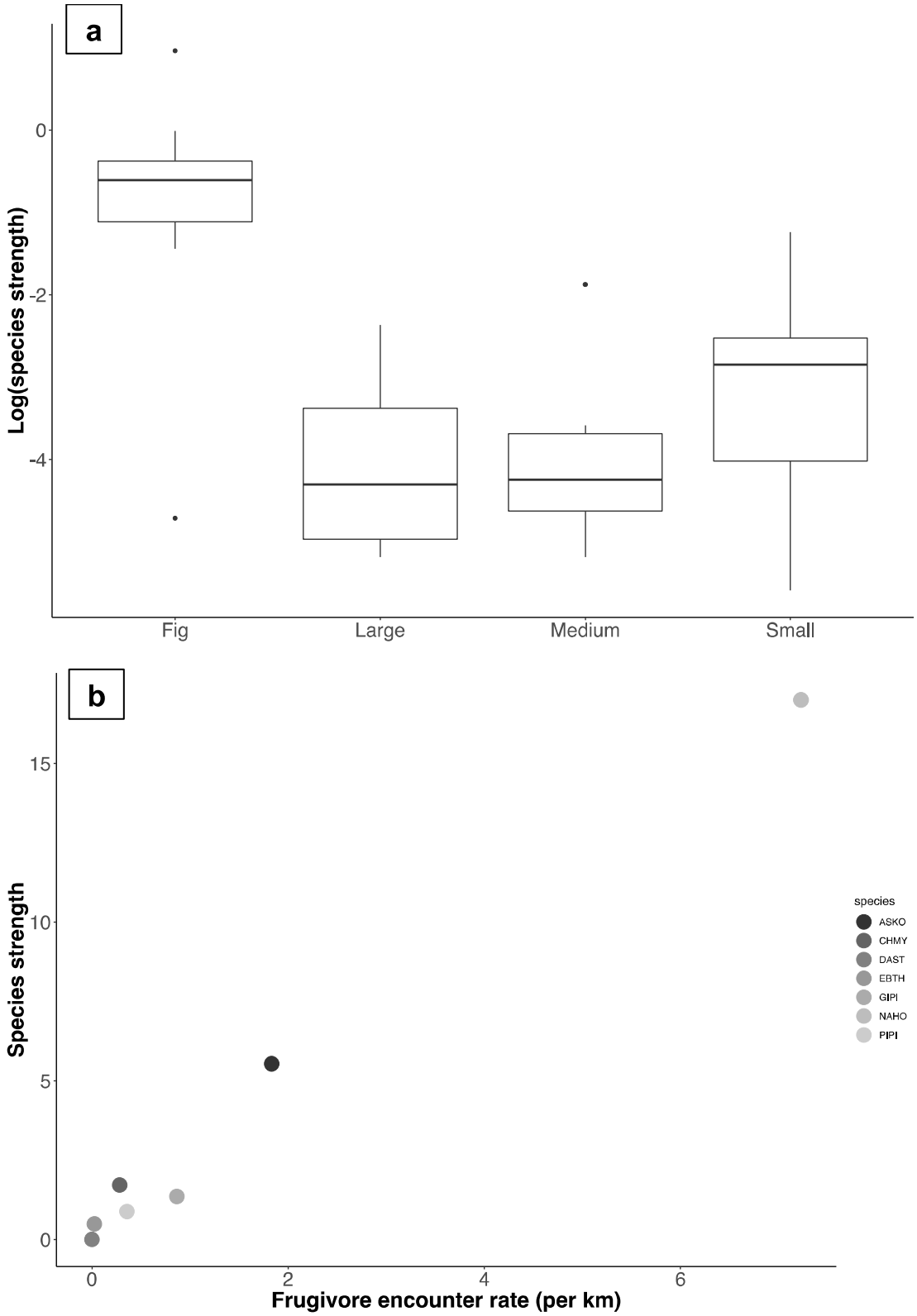
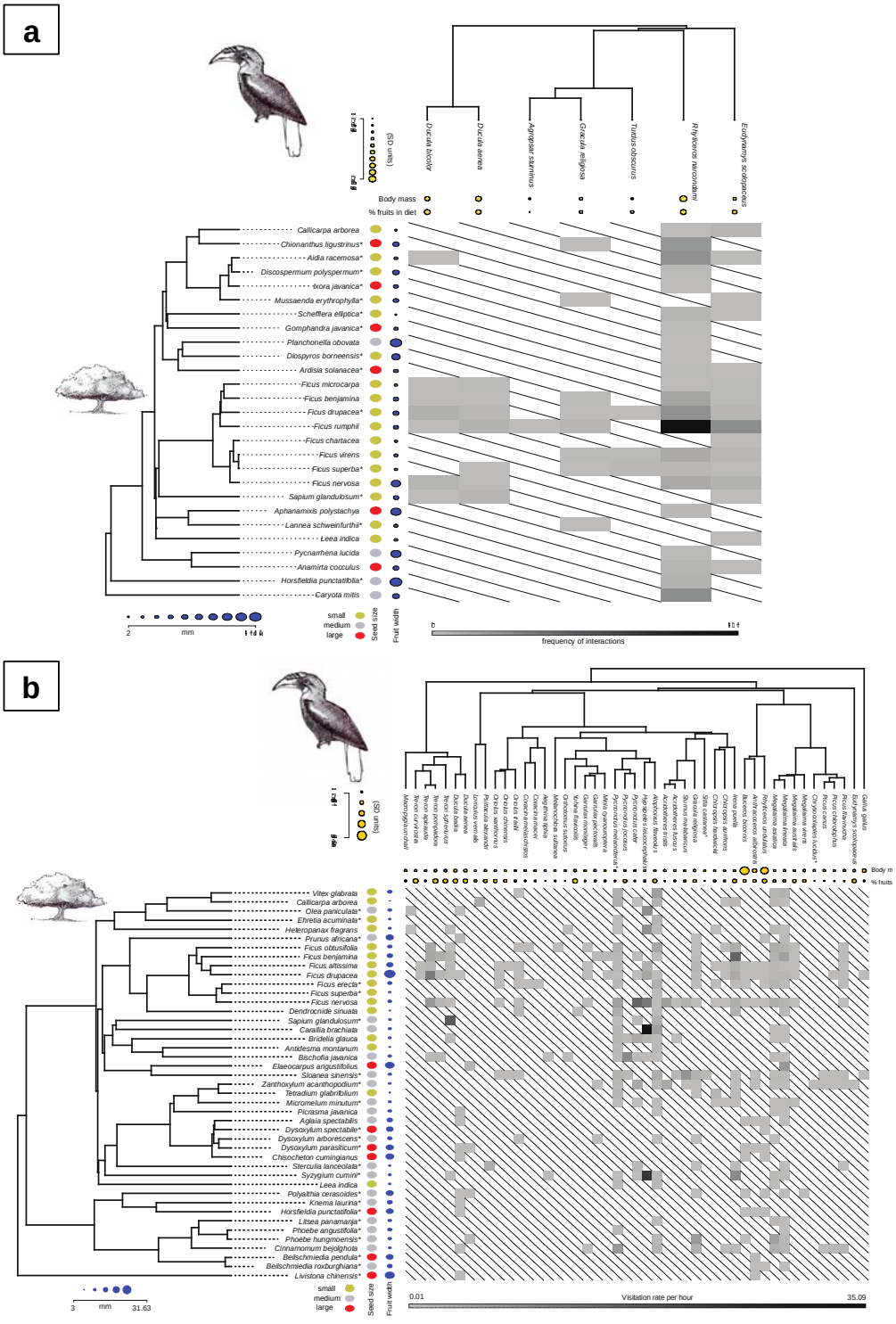

a
Log(species strength)
0
-2
-4
Fig
Large
Medium
Small
b
Species strength
15
10
5
0
0
2
4
6
Frugivore encounter rate (per km)
species
ASKO
CHMY
DAST
EBTH
GIPI
NAHO
PIPI

Figure 4.


a
Ducula bicolor
Ducula aenea
Aplonis panayensis
Gracula religiosa
Turdus obscurus
Rhyticeros narcondami
Eudynamys scolopaceus
(SD sum)
Body mass
% fruits in diet
Callicarpa arborea
Chionanthus ligustrinus*
Aidia racemosa*
Discospermum polyspermum*
Ixora javanica*
Mussaenda erythrophylla*
Schefflera elliptica*
Gomphandra javanica*
Planchonella obovata
Diospyros borneensis*
Ardisia solanacea*
Ficus microcarpa
Ficus benjamina
Ficus drupacea*
Ficus rumphii
Ficus chartacea
Ficus virens
Ficus superba*
Ficus nervosa
Sapium glandulosum*
Aphanamixis polystachya
Lannea schweinfurthii*
Leea indica
Pycnarrhena lucida
Anamirta cocculus
Horsfieldia punctatifolia*
Caryota mitis
2
mm
small
medium
large
Seed size
Fruit width
frequency of interactions
b
(SD sum)
Body m
% fruits
Vitex glabrata
Callicarpa arborea
Olea paniculata*
Ehretia acuminata*
Heteropanax fragrans
Prunus africana*
Ficus obtusifolia
Ficus benjamina
Ficus altissima
Ficus drupacea
Ficus erecta*
Ficus superba*
Ficus nervosa
Dendrocnide sinuata
Sapium glandulosum*
Caralliа brachiata
Bridelia glauca
Antidesma montanum
Bischofia javanica
Elaeocarpus angustifolius
Sloanea sinensis*
Zanthoxylum acanthopodium*
Tetradium glabrifolium
Micromelum minutum*
Picrasma javanica
Aglaia spectabilis
Dysoxylum spectabile*
Dysoxylum arborescens*
Dysoxylum parasiticum*
Chisocheton cumingianus
Sterculia lanceolata*
Syzygium cumini*
Leea indica
Polyalthia cerasoides*
Knema laurina*
Horsfieldia punctatifolia*
Litsea panamanja*
Phoebe angustifolia*
Phoebe hungmoensis*
Cinnamomum bejolghota
Beilschmiedia pendula*
Beilschmiedia roxburghiana*
Livistona chinensis*
3
mm
31.63
small
medium
large
Seed size
Fruit width
0.01
Visitation rate per hour
35.09