

Impact of habitat fragmentation on plant-frugivore
interactions in lowland tropical forests of Upper-
Assam, North East India

DISSERTATION SUBMITTED TO SAURASHTRA UNIVERSITY, RAJKOT

IN PARTIAL FULFILMENT OF

MASTER'S DEGREE IN WILDLIFE SCIENCE

2018 - 2019

By

ABIR JAIN

Under the supervision of

DR. NAVENDU PAGE

DR. G. S. RAWAT

DR. ROHIT NANIWADEKAR



भारतीय वन्यजीव संस्थान
Wildlife Institute of India



“Every fruit has its secret”

- *Figs (D.H. Lawrence, 1928)*



Dedicated to the Hornbills of north-east India and my family



भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that **Mr. Abir Jain** has carried out an original piece of research from the Wildlife Institute of India, titled "**Impact of Habitat Fragmentation on Plant-Frugivore Interactions in Lowland Tropical Forests of Upper Assam, North-East India**", in partial fulfilment of a Master's Degree in Wildlife Science from Saurashtra University, Rajkot, India. The study was carried out under our supervision from December 2018 to June 2019. We hereby certify that this work has not been submitted for any other degree to any University.

Dr. Navendu Page
Scientist C

Dr. G.S. Rawat
Scientist G

Date: 30th June 2019

Place: Dehradun

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून - 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फ़ैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई-मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

DECLARATION

I, **Abir Jain**, hereby declare that the research work titled “**Impact of Habitat Fragmentation on Plant-Frugivore Interactions in Lowland Tropical Forests of Upper Assam, North-East India**” carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of work. These study was carried out under the supervision of Dr. Navendu Page and Dr. G.S. Rawat at the Wildlife Institute of India and Dr. Rohit Naniwadekar of The Nature Conservation Foundation from December 2018 to June 2019. I also declare that this work has not been submitted for any other degree of any university.

Date: 30th June, 2019

Place: Dehradun

ACKNOWLEDGEMENTS

It is early July of 2019 in Dehradun, skies grey and blue. The time of the year when thousands of *Shorea* seeds are ready and loaded to gracefully take off in batches, as the monsoons are beginning to arrive. Swirling in the air, racing against both, gravity and time, spinning away from their parent tree, only to land somewhere from where they can germinate. I wondered if we are any different? As I stood under one of my favourite ‘Sal’ trees taking a moment to watch this spectacle of nature.

Undeniably, it is impossible to make any journey count without the push of some really high-spirited people who have stood by and sailed alongside at different points of time, bringing this piece of work to a stage where it stands today.

I am immensely grateful to my supervisors whose seamless patience, tireless dedication and childlike excitement for learning from every little thing, has made this journey one of the best learning experiences so far. They have offered teachings that will last a lifetime. I am truly grateful to Rawat Sir for his overarching wisdom, warm smile, vast knowledge and radiating kindness. I have felt inspired since the day I first walked with him in the forest. Navendu, for he has been there right from the conceptualisation of the thesis channelizing my scattered thoughts, for his ever-humble nature, patient listening, delicious home food and his many visits to the hostel to resolve even the tiniest of problems. Rohit, for his undying hope in me. For trying every possible way to make my thoughts marginally ‘nested’. For days and nights of worrying, even on my behalf, for high ‘connectance’ by being available at any time and at any place, for hours and hours of skype calls, for carefully guiding me and pointing even the smallest of my mistakes, for being considerate, always. For sharing the excitement, for his stress-busting songs to the lord when things went out of hand, and for all the fun we had on field and otherwise, and for the common love for hornbills. Thank you for being there like an elder brother and always reassuring me during dull days. I don’t think one could ever ask for more. I am extremely lucky to have you all as my supervisors. I thank Sartaj who also visited us in the field and reminded us to keep in mind that “there is as much on the forest floor as there is above”.

I extend my sincere gratitude to the Assam Forest Department, the CWLW, DFO Dibrugarh, Digboi and Doomdooma division, range officers, beat officers and beat guards who have helped us and facilitated our stay and study at various occasions.

I was extremely lucky to be assisted by extremely cheerful, high-spirited sincere, hard-working and enthusiastic Khageshwar. This study would have been extremely difficult to achieve without him. He has taken immense care of us like family and was thoughtful about the tiniest of things during field days. He is a true jungle man with an innocent heart and we have learnt a lot from him during our walks in the forest and otherwise. It was nearly impossible to detect some ‘Gutis’ (fruiting plants) without his watchful eyes, given my partial colour-blindness. My sincere gratitude to him and his beautiful family. I also thank ‘accha aadmi’ Porag, Jakir, Bablu, and their families for helping us in the field. I am also grateful to Kashmira and Narayan for helping us kick-start the study.

I thank the people of Assam for their unending hospitality, our Assamese family of the ‘contiguous forests’ – ‘Thapas’ who adopted us just as we moved to a strange land and were new to the surroundings. Smiti, our tiny little bundle of joy, who was filled with seamless curiosity about literally everything, her great sense of humour and for teaching us so many things; Pinky aunty, for very delicious food, kindness and lots of good talks; Thapa da for all the fun times and facilitating our study in all aspects, Dadiji and the newly arrived

little one for spreading joy. Our family of the ‘fragmented forests’ – ‘Phukons’ for making us a part of their house, for all the tasty food they stuffed us with, for all the generosity they bestowed upon us and long talks on life lessons. It did not feel one was away from parents. I thank Bhaskar Bora and his team, Nayan da and Dhruvo da for helping us out at several occasions.

I find myself extremely fortunate to have shared these four months of field work with Sumashini and Sutirtha. It would have been dull without their lovely company, Sunday French toast, cooking, countless rounds of chai, coffee, samosas and lot of good talks. I am truly grateful to Suma, who has been a constant source of inspiration, strength, hard work, happiness and warmth during the last two years. I thank her for her camaraderie, for taking so much care, all the moral support, for sharing endless laughter, for bearing with me and needless to mention, for walking together more than 600 kilometres in these beautiful rainforests, which was truly a delightful experience. Shunting between seven field sites thrice during four months and covering half of upper Assam, would have become an absolute nightmare if I were to do it independently. Learning would have been half as enjoyable and days half as merry if it was not with you.

My warmest gratitude to XVI MSc., the people who closely shared this journey. It was unthinkable without their love, support and understanding. I thank Kush, for always motivating me to do the best and beating me up whenever necessary; Bhavya, for sitting on my head, making mind-maps and taking so much care; Sakshi for lifting my spirits when I needed the most; Nisam for being a true study-buddy; Aaranya for always keeping others first; Doli for keeping an eye and supply of infinite food; Mohit and Laxmi for spreading happiness always; Abhishek for his simplicity; Himanshu for lifting our moods with his sketches; Subhashini for being a good pet; Varun for selflessly helping everyone with his godly abilities and making seemingly difficult things much easier and sometime much more difficult; Indira for reminding us of little things in nature; Pratik for triggering critical thinking; Siva for his dedication. And to the unending supply of coffee, for bringing us all together. To all the beautiful times we’ve spent together, these two years have been my best so far.

Many thanks to Rajat from where it all began, Ninad, Neeraj, Ankita and Pritha who have been a great support throughout.

I thank Qamar sir, Jhala sir, Manoj sir, Abhijit sir, Gopi sir, Sutirtho sir, Malvika ma’am and many other faculty members at the institute who encouraged me always.

Just as how I watched the ‘Sal’ seed rain looking back at fond memories, I am grateful to Mashumi, who has effortlessly monitored my whereabouts and been there with me closely in this journey. I thank her for everything.

Finally, I thank my pillar, my family: Acchi mumma, Mumma, Papa, Ameya, Baanu and everyone else; My extended family: The Chitales for being so understanding and supportive always. Thank you also, for visiting me to my field site. It was heart-warming to have you around.

- Abir

CONTENTS

INTRODUCTION	1
TROPICAL FORESTS AND SEED DISPERSAL.....	1
FOREST FRAGMENTATION AND TROPICAL FORESTS.....	2
NETWORK APPROACH.....	2
BACKGROUND AND STUDY QUESTIONS	5
STUDY AREA	6
LOCATION, AREA AND PHYSICAL FEATURES.....	6
HISTORY AND ANTHROPOGENIC DISTURBANCE.....	6
GEOGRAPHY	7
VEGETATION.....	7
BIODIVERSITY.....	8
CLIMATE.....	8
METHODS.....	11
OBSERVATION OF PLANT-FRUGIVORE INTERACTIONS	11
VEGETATION SAMPLING.....	11
MORPHOLOGICAL TRAITS.....	12
ANALYSIS	12
RESULTS.....	14
PLANT-DISPERSER INTERACTIONS	16
DISCUSSION.....	25
COMMUNITY LEVEL PATTERNS.....	25
OF PLANTS, THEIR HABITS AND THEIR ROLE IN STRUCTURING PLANT-DISPERSER COMMUNITIES	26
OF BULBULS, BARBETS AND HORNBILLS	28
WAY FORWARD.....	30
APPENDICES.....	31
REFERENCES	35

LIST OF FIGURES

Figure 1: Structure of a simple unweighted network depicting plants on the left, seed-dispersers on the right and links indicate interacting species (Modified from Garcia 2016).3

Figure 2: (a) Nested community and (b) Distinct sub-communities of interacting species. Matrix depicts, plants arranged in columns, seed-dispersers in rows and shaded cell represents interacting species.....3

Figure 3: Map of study sites in the fragmented landscape of Brahmaputra valley, upper Assam. The ‘large ($\geq 100 \text{ km}^2$)’ sites namely Jeypore and Soraipong represent the contiguous forests. Sites Kakojan and Doomdooma represent the ‘medium (24 km^2)’ forest fragments and sites Borajan and Bherjan represent the ‘small (3 km^2)’ forest fragments. For further details refer table 2.....9

Figure 4: Unweighted plant-seed disperser networks of contiguous and fragmented forests. In each network, nodes on the left shows plant species and nodes on the right shows frugivore species; thickness represent the number of mutualist partners. The yellow nodes are species unique to the contiguous forests, blue nodes are common species and the red ones are the unique species to the fragments. Full bird and plant names associated with codes can be found in appendices.15

Figure 5: Percentage of total interactions observed on different plant habit types in contiguous and fragmented forests.....16

Figure 6: Frequency of observed interactions on tree species in contiguous forests (left) and fragments (right). All the ficus species (highlighted above) were merged to check their contribution from the total number of observed interactions.15

Figure 7: Mean ($\pm \text{SE}$) of Degree, Betweenness and Closeness across two habitat types for plant habits (climbers, epiphytes, shrubs and trees). Highlighted values depict higher values of degree and betweenness centrality for climbers compared to other plant forms.19

Figure 8: Degree, Betweenness and Closeness across two habitat types for frugivore family. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.21

Figure 9: Degree, Betweenness and Closeness across two habitat types for large-and small-bodied frugivores. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.22

Figure 10: Degree, Betweenness and Closeness across two habitat types for frugivore family. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.24

LIST OF TABLES

Table 1. Details of study sites, their area (km²) and protection status (refer fig. 3 for map)7

Table 2. Sampling effort across the small fragments, medium-sized fragments and contiguous forests10

Table 3. Attributes of vegetation structure of the different study sites.... Error! Bookmark not defined.

Table 4: Network level properties of an unweighted network generated from the interactions observed in the contiguous forests and fragments.17

Table 5: Observed values and mean of the 1000 null model predictions of NODF and connectance.....18

LIST OF APPENDICES

<i>Appendix 1: List of avian frugivore species that participated in the Network during the study period.</i>	31
<i>Appendix 2: List of fruiting plant species that participated in the Network during the study period.</i>	33
<i>Appendix 3: Attributes of vegetation of different study sites</i>	35

EXECUTIVE SUMMARY

1. Tropical forests are considered the storehouse of biodiversity. One of the key ecosystem processes that governs the diversity of tropical trees is seed dispersal. Tropical forests globally face deleterious effects of habitat fragmentation such as loss of habitat area, reduced species richness and altered community composition. Forest fragmentation can also alter mutualistic interactions between plants and seed dispersers, disrupting key ecosystem processes like seed recruitment and regeneration. In the past century, logging, habitat conversion to tea plantations and agricultural fields have resulted in the fragmentation of the last remaining lowland tropical forests of Upper Assam in north-east India. However, these isolated forest fragments might also hold a great potential to preserve native biodiversity distributed across patches. There is paucity of information on impacts of habitat fragmentation on plant–seed disperser interactions from Asia.
2. In this study, I investigate the impacts of habitat fragmentation on plant-disperser communities. The impacts were assessed at the level of the community and at the level of species guilds (body size, habits, and families).
3. The plant-frugivore interactions were recorded by systematically walking 27 trails across two habitat categories: contiguous forest sites (n=2) and fragmented sites (n=4) over the duration of four months. Spot census was carried out to record interactions between a fruiting plant and frugivores. Fruit handling behaviour of birds and fruit crop size of plants were also recorded. Plants and seed dispersers that interact with one another, forms a network.
4. I constructed presence-absence networks for each habitat type, which represents all plant-seed disperser interactions recorded in the contiguous forests and the forest fragments. ‘Network-level’ properties were obtained to understand the influence of fragmentation on plant-seed disperser communities and ‘Species-level’ properties were obtained to assess the roles of species guilds in each of these communities.
5. Although, the networks for contiguous and fragmented forests were similar in terms of total number of mutualist species participating in its organisation, their composition was different. On an average, frugivores had one plant partner more in the contiguous forest, while plants had three frugivore partners more in the forest fragments.

6. The relative importance of the different plant and bird families differed across contiguous and fragmented forests. *Ficus* spp. constituted an important resource for frugivores especially in the forest fragments. Fruiting climbers of the family Rosaceae and Urticaceae had the greatest number of frugivore partner species and were an important plant group in both contiguous and fragmented forests. Smaller-bodied frugivores, particularly barbets and bulbuls had the greatest number of plant partner species and were the key seed-dispersers in both contiguous and fragmented. Large-bodied frugivores like hornbills fed mostly on large-seeded fleshy fruits and they are able to persist in fragmented forests as has been documented in Western Ghats. This study highlights limited impacts of habitat fragmentation on plant-seed disperser communities of this landscape

Keywords: Plant-seed disperser interactions, habitat fragmentation, tropical forests, bipartite networks.

INTRODUCTION

Tropical Forests and Seed Dispersal

Tropical forests occupy only 6-7% of earth's surface, harbouring about 60% of the world's terrestrial biodiversity which includes 40,000 to 50,000 species of trees (Rocha-Santos et al., 2016; Slik et al., 2015). Remarkably, only a square kilometre plot in rainforests of Borneo and a quarter of a square kilometre plot in Ecuador can support over one thousand species of trees with diameter more than 1cm at breast height (Wright, 2002). More than 75% of tropical trees are dependent on seed dispersal by animals (Terborgh, 1992) and majority of vertebrate biomass is supported by fleshy fruits (Fleming, Randall, & Whitesides, 1987). Seed-dispersing animals facilitate coexistence of many plant species by reducing density-dependent mortality under the parent tree. Allelopathy, intra-specific competition and host-specific pest facilitation (the Janzen-Connell effects) also contribute in providing space for less successful species and constraining space for the abundant ones (Janzen, 1970; Wright, 2002). These mutualistic interactions between plant and pollinators or plant and seed dispersers have had a major role in evolutionary processes and generation of earth's biodiversity for over 70 million years (Olesen et al., 2007; Estrada & Fleming, 1986).

Fruits vary considerably in size, crop mass, colour, odour, nutrients, fruit position and texture, which govern frugivore choice and their ability to handle, swallow and process them (Shanahan et al., 2001). Frugivores may be characterised as legitimate dispersers, pulp consumers or opportunistic seed-predators depending on how they handle fruits (Jordano, 2000). Animals that disperse the seeds unharmed, away from the parent plants, can be considered seed dispersers (Schleuning et al., 2011). Previous studies have shown that the overlap in the diet (shared plant species) between frugivorous birds and mammals can be limited indicating that birds could play an exclusive role in seed dispersal of certain plant species (Jordano, 1995; Sekercioglu, 2006). In a global review on consumption of *Ficus* species by vertebrate frugivores, Shanahan et al., 2001 recorded 1236 animal species consuming figs out of which 997 were bird species belonging to a large number of genera from various families. This is also suggestive of the fact that a majority of frugivores are birds, highlighting their important role as avian seed dispersal agents in the case of figs.

Forest Fragmentation and Tropical Forests

Tropical forests worldwide have witnessed severe fragmentation with a gross loss of about 8.0 million hectares per year (Achard et al., 2014). As a consequence, most tropical forests today exist as fragments interspersed in a mosaic of agriculture, plantations and other non-forest human land uses (Osuri et al., 2017). Forest fragmentation and associated edge effects can have pervasive impacts on forest structure and plant-animal communities. Long-term studies on fragmentation suggest that short-lived early successional pioneer trees replace shade-tolerant plants, old-growth emergent trees and high climbing lianas, often leading to the simplification of habitat and destabilisation of carbon stocks across fragments (Laurance et al., 2006; Rocha-Santos et al., 2016). Studies have reported that loss of important large-bodied seed dispersers results in higher vulnerability of large-seeded fruiting trees (Chen et al., 2017; Cramer et al., 2007; Wotton & Kelly, 2011). Fragmentation reduces the visitation rates of frugivores on fruiting trees, particularly of large-seeded plants (Markl et al., 2012). Majority of the studies that have investigated the impacts of forest fragmentation on seed dispersal have focused on a sample of species (one to four species) and community-wide approaches have been limited. Community-wide approaches facilitate identification of changes in the broad patterns of seed-bird disperser interactions. Forest remnants may contribute significantly to preserving native biodiversity and maintaining connectivity through shared ecological interactions across large areas (Sharma & Sinha, 2012).

Network Approach

Species of interacting plants and animals form a network. Assessing these networks can allow us to systematically examine interactions of plant-animal communities. Bipartite networks enable an understanding of complex structure and the functioning of plant-frugivore interactions in ecological communities. They can be constructed based on presence-absence data (unweighted network) or data that incorporates measures like visitation or fruit removal rates of frugivores (weighted networks) (García, 2016).

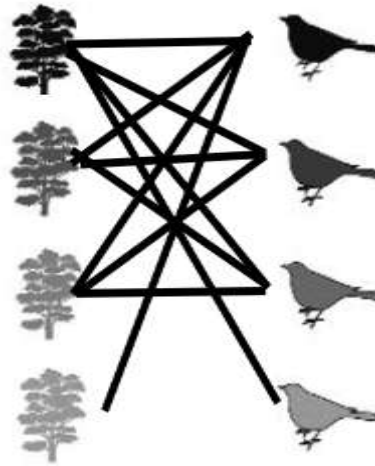


Figure 1: Structure of a simple unweighted network depicting plants on the left, seed-dispersers on the right and links indicate interacting species (Modified from Garcia 2016).

Network analysis aids better understanding of plant-seed disperser interactions at the level of communities (networks-level properties) or at the level of species (species-level properties). These properties are a measure for drawing community-level patterns and determining roles of individual species or guilds in network organisation. Some commonly reported network and species-level properties that were used for this study are explained in detail on Page No. 13. Network structure can be 1) highly heterogeneous with only a few species constituting a majority of interactions 2) nested, wherein specialist species (species with lowest partners) interact mostly with species with which generalist species (species with highest partners) also interact (Fig. 2a), 3) modular, forming sub-groups of interacting species that interact much more with each other than to members of other sub-groups (Fig. 2b) (Pedro Jordano, Bascompte, & Olesen, 2003; Olesen et al., 2007).

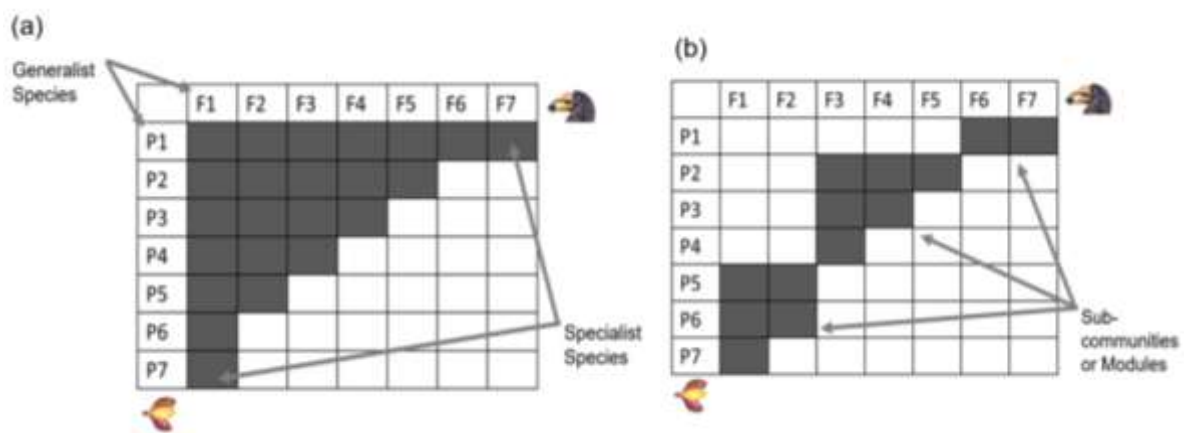


Figure 2: (a) Nested community and (b) Distinct sub-communities of interacting species. Matrix depicts, plants arranged in columns, seed-dispersers in rows and shaded cell represents interacting species.

Nested pattern is considered to improve species persistence since the loss of specialist partner species might be compensated by another generalist partner species, thereby having a minimal impact on the network structure (Garcia, 2016). Similarly, modularity might also prevent extinction cascades, since loss of species will only impact the sub-group within which it belongs and not the wider network as the sub-groups are weakly linked with one another.

Fruit-eating birds share a strong functional relationship with fleshy-fruited plants corresponding to their functional traits (Schleuning et al., 2014). For eg. large-seeded fleshy fruits can only be dispersed by large-bodied birds with large gape size. Forest specialists were restricted only to closed canopy forests and undisturbed habitats (Olesen et al., 2007). However, generalist species formed the core of shared interactions in both disturbed and undisturbed habitats maintaining gene flow across patches (Palacio et al., 2016). Shared interactions promote network cohesiveness (Freeman & Mulholland, 1979) and community stability (P Jordano et al., 2010). A recent study of plant-frugivore interactions from a fragmented landscape in South America revealed loss of interactions with large-bodied, specialist frugivores such as toucans from smaller fragments (Emer et al., 2018). However, certain interactions with small-bodied, generalist frugivores persist in smaller fragments (Emer et al., 2018). This suggests that avian frugivores act as mobile links among weakly connected forest fragments and play an important role in ecosystem prevalence by maintaining shared ecological interactions between forest fragments as has been demonstrated by hornbills in Africa (Lenz et al., 2015). Therefore, network approach is a useful tool for understanding impacts of habitat fragmentation.

The research on ecological networks has advanced considerably in recent years and is now being studied widely to represent baseline information for understanding community dynamics (García, 2016). Network-level patterns not only represent community-wide interactions organised in nested or modular networks but also provide us insights on the roles that individual species contribute in network resilience by identifying their shared ecological functions (Hagen et al., 2012). Observing plant-frugivore interactions and comparing their network characteristics across fragmenting would therefore help us observe responses of mutualistic interactions to effects of fragmentation in lowland tropical evergreen forests of North eastern India.

Background and study questions

Habitat conversion to tea plantations and agriculture, planned felling operations until late 1900s, oil and natural gas extraction during the past two centuries have led to drastic shrinkage and fragmentation of what was once a large tract of contiguous forests. These last remaining lowland tropical wet evergreen forests of Upper Assam now exists only in pockets of few large and several forest fragments of varying sizes (Sharma & Sinha, 2012). They are isolated by a surrounding matrix of large areas of tea plantations, agricultural fields, human settlements and continue to face high pressures of degradation (Kakati et al., 2005). However, remnant patches act as the last refuge for many native and endemic species of flora and fauna of this region (Sharma & Sinha, 2012). This makes the study site ideal to address my research questions.

This study aims to understand the impacts of habitat fragmentation on plant-seed disperser communities in the lowland tropical wet evergreen forests of Upper Assam. Specific objectives are to evaluate the impacts of habitat fragmentation on plant-disperser communities at the level of communities and at the level of species in both contiguous forests and forest fragments.

Objective 1. To compare network-level properties such as nestedness, connectance, generality and vulnerability (Page No.13) of contiguous forests to that of the fragmented forests.

I expected that plant-disperser communities in fragments will be a nested subset of that of the contiguous forests since interactions between plants and frugivores will be lost from the fragments.

Objective 2. To compare species-level properties viz., degree, betweenness centrality and closeness centrality (Page No. 14) and identify unique interactions across the two treatments. To compare these species-level properties across species traits and across families.

This approach will help determine how species-level properties change across fragmented and contiguous forests and identify crucial functional groups that help sustain interactions in fragmented and contiguous forests. I expected large-frugivores and large-seeded plants to be affected in fragmented forests and correspondingly their functional roles will be comprised in these modified habitats.

STUDY AREA

Location, area and physical features

The field work of the study was carried out between December 2018 and April 2019 in six sites of what were originally lowland tropical wet evergreen forests located under Dibrugarh, Tinsukia and Doomdooma districts of Assam. The sites were located between 95° 21'28.3 to 96° 00' 51.1 E and 27° 05' 35.2 to 27° 45'11.2 N. The forest reserves were chosen after a reconnaissance survey and were categorised into three size classes – small (area: <5 km²), medium (area: 20 – 30 km²) and large contiguous forests (area: ≥100 km²) (Table 1.). Dehing Patkai Wildlife Sanctuary along with Jeypore Reserve Forest represent the large contiguous forest which is about 200 square kilometres, contiguous with the foothills of Patkai Range on India's north-eastern border with Myanmar (Kakati et al., 2005). They are surrounded by broken, isolated smaller fragments with various degrees of degradation and protection.

History and anthropogenic disturbance

As a consequence of region's complex history (pre-colonial, colonial and post-colonial) and major upheaval in terms of economy and policy that led to demographic changes in the region's ecology over the past centuries. During these periods, expansion of tea gardens and associated industries, heavy influx of immigrants from neighbouring countries, economic growth associated with rampant extraction of natural resources such as natural gas, oil, coal, wildlife and forest timber for rail sleepers, boat building and construction resulted in major destruction in region's ecology (Sharma & Sinha, 2012).

Of the selected sites, the large Jeypore Reserve Forest and Dehing Patkai Wildlife Sanctuary best represents the regions ecology and face relatively less anthropogenic disturbance today, as compared to its past (Kakati et al., 2005). We encountered some instances of illegal logging and hunting close the political border between the Indian states of Assam and Arunachal Pradesh. Unfortunately, due to lack of forest staff, poor implementation of forest laws and as a consequence of being surrounded by human habitation and tea gardens on all sides, the fragment reserves continue to face high pressures of degradation. We observed instances of illegal felling using mechanized chainsaws, wood-cutting and catapult hunting by individuals from the surrounding villages. Some small fragments that we surveyed were extremely degraded.

Table 1. Details of study sites, their area (km²) and protection status (refer fig. 3 for map)

Sites	Size Class	Area (km ²)	Protection Status
Bherjan	Small	3	Wildlife Sanctuary
Tokoni	Small	3	Reserved Forest
Kakojan	Medium	23.47	Reserved Forest
Doomdooma	Medium	24	Reserved Forest
Dehing Patkai	Large	≥100	Wildlife Sanctuary
Jeypore	Large	≥100	Reserved Forest

Geography

With River Buridehing cutting through the two large forest sites (Dehing Patkai and Jeypore Reserve Forests), the forests encompass mostly undulating terrain consisting of low-lying hills characterised by several perennial streams, called nullahs, running in the through hill valleys. The ridge-tops are characterised by emergent and mid-storey rainforest trees. Although, reserves in the fragments were relatively flat, locally called ‘kurkani’ with fewer streams with comparable vegetation composition. The altitude varied from 120 m in the smallest reserve up to 300 m in the contiguous forests. Soil type is old alluvium of the Brahmaputra and Buridehing rivers, the former being almost neutral while the latter being acidic soil. The southern foothills along River Buridehing is composed of Upper tertiary rocks, the Tipam sandstone and are rich in oil deposits (Kakati et al., 2005).

Vegetation

The forests of the study area were classified by (Champion & Seth, 1968) as Northern Tropical Wet Evergreen Forest (1B). The forest vegetation is divisible into three vertical strata: with emergent dipterocarps such as *Dipterocarpus macrocarpus* and *Shorea assamica* that form the top canopy standing upto 40-50 m tall, middle canopy (~30 m) is formed by *Mesua ferrea*, *Vatica lanceaefolia* (another dipterocarp) or otherwise miscellaneous tree species and woody climbers. Trees are mostly evergreen, common ones include *Sapium baccatum*, *Magnolia* spp., *Terminalia myriocarpa*, *Castanopsis indica*,

Talauma hodgsonii, *Elaeocarpus floribundus*, *Dillenia indica*, *Altingia excelsa*, *Dysoxylum spp.*, *Ficus spp.*, *Artocarpus lakoocha*, *Bischofia javanica*, *Lagerstroemia flos-reginae*, *Terminalia bellerica* and *Duabanga grandiflora* among many others. The understorey is generally sparse, with various ferns and woody shrubs. Valleys and slopes are dominated by bamboos, ferns, canes and wild banana.

Biodiversity

The study area is part of the Indo-Myanmar Biodiversity Hotspot. This region alone sustains around 10,000 to 20,000 plant species, 520 amphibian and reptile species, 1,200 bird species, 430 mammal species, and between, many of them endemic and endangered (Sharma & Sinha, 2012). Jeypore-Dehing forests provides habitat to seven species of wild cats (Golden Cat, Fishing Cat, Marbled Cat, Tiger, Clouded Leopard, Common Leopard and Leoaprd Cat), several other mammals like Western Hoolock Gibbon, Slow Loris, Binturong and birds like, Peacock Pheasant, White-throated Brown Hornbill, Silver-breasted Broadbill, Malayan Night Heron, etc to name a few.

Climate

The area is characterized by high humidity and rainfall (2226 to 3644 mm). It receives rainfall from the north-east and south-west monsoon between June to November. There is occasional rainfall between December to February and this period is mostly dry. The area receives thunderstorms and summer showers between March and May. Temperatures in the area range between 6 – 38 °C (Kakati et al., 2005).



Figure 3: Map of study sites in the fragmented landscape of Brahmaputra valley, upper Assam. The 'large ($\geq 100 \text{ km}^2$)' sites namely Jeypore and Soraipung represent the contiguous forests. Sites Kakojan and Doomdooma represent the 'medium (24 km^2)' forest fragments and sites Borajan and Bherjan represent the 'small (3 km^2)' forest fragments. For further details refer table 2.

Table 2. Sampling effort across the small fragments, medium-sized fragments and contiguous forests

Sites	Contiguous		Total	Medium		Total	Small		Total
	Jeypore	Soraipong		Doomdooma	Kakojan		Tokoni	Bherjan	
No. of unique trails	9	2	11	5	7	12	2	2	4
Unique trail length (km)	26	4	30	8	15	23	2	3	5
Effort (km)	145	30	175	55	61	116	10	34	44
Effort (h)	132	22	154	47	78	125	9	27	36
Sampling days	43	6	49	15	19	34	6	5	11

METHODS

Observation of Plant-Frugivore Interactions

Twenty-seven trails were identified across different contiguous and fragmented sites (Table 2). The length of the trails varied from 1 – 5 km (Table 2). Considering the differences in timings of sunrise over four months, the trails were walked for 2-4 hours between 0500 – 1230 h to coincide with the peak frugivore activity. Trails were walked at a slow pace (~1 km per h). The total effort across the different contiguous and fragmented sites was 335 km (Table 2). The effort was spread over three rounds of sampling and was kept comparable across contiguous and fragmented forests (Table 2). Same trails were walked repeatedly over different months across the different sites to account for changes in seasonality and phenology of fruiting species.

During the trail walk, on encountering frugivore activity on fruiting trees, I performed spot censuses to document plant-avian seed disperser interactions following Palacio et al., (2016). The mean duration of spot census was 6 minutes (ranging between 1 – 30 min). During the spot census, I recorded all the frugivores on the fruiting trees. I recorded, the tree and frugivore species identity, number of frugivores, start and end time of the scan. I also performed focal scans to document the fruit handling behaviour of the frugivore. During the focal scans, I recorded start and end time of focal scans and the number of fruits dropped, pecked or swallowed. An avian frugivore was classified as a seed disperser only if it was seen swallowing the fruit. Observations were carried out using 10 x 42 Nikon Monarch binoculars. I also recorded fruit crop size of all the plants (except *Rubus lucens*, *Poikilospermum* sp. and other scandent climbers/epiphytes alike). Spot scans were carried out following (Davidar & Morton, 1986; Slik et al., 2015). I also recorded all plant-avian frugivore interactions outside the sampling period following similar protocol.

Vegetation sampling

To determine tree density, basal area, tree height and plant species composition, I employed the point-centred quarter (PCQ) method (Cox, 2002) at every 100 – 200 m interval on the trail. In each quarter, I recorded two trees, one ≥ 30 cm GBH (girth at breast height) and one between 10 – 30 cm GBH. The latter class helped assess plant regeneration. Tree height and girth was recorded for each of the sampled trees and canopy cover was also estimated using Canopeo App on an android phone (OnePlus 5). Additionally, at each PCQ location,

identity and count of trees that were larger than 25 cm GBH were recorded in 10 m radius to better capture the plant species richness. Number of lianas were also recorded to estimate their densities. Plant species were identified with the help of local floras (Kanjilal & Das, 1934-40) and other monographs). Floral and vegetative parts of unidentified species were given code names in the field and carefully photographed for subsequent identification with the help of experts and verification from the standard herbaria at Forest Research Institute of India (FRI) and Wildlife Institute of India (WII).

Morphological traits

At least ten fruits of each plant species on which the interaction was recorded, were collected. Fruit length, fruit width, number of seeds, seed length and seed width were measured using a digital Vernier calliper (Mutitoyo). We classified seeds as small-seeded, medium-seeded, and large-seeded following (Naniwadekar et al., 2019). Body size and body mass information of birds was collated from (Wilman et al., 2014) and were classified as large-bodied and small-bodied following (Vidal et al., 2014).

ANALYSIS

The plant-disperser interactions were arranged in a matrix and two unweighted (presence-absence) networks were constructed, one for contiguous forests and another for all the four forest fragments put together. Only frugivores that were seen swallowing the fruits and seeds were considered as seed-dispersers, except in the case of *Ficus* spp., whose tiny seeds are ingested even when their fruit is pecked at. Analysis was carried out at the level of the networks and at the level of species (birds and plants). For network-level analysis, measures like *NODF* (*nestedness*), *network connectance*, *generality* and *vulnerability* were used to compare network structure of contiguous forest sites with that of the fragmented sites. For species-level analysis matrices like *degree*, *betweenness centrality* and *closeness centrality* were used. These measures were compared across contiguous and fragmented forests for different plant and seed-disperser groups. All indices have been explained in greater detail in the subsequent sections. Attributes of vegetation structure like stem density and basal area were also calculated following (Mitchell, 2010).

Network-level

To see how communities are organized in both habitat categories, I compared values obtained from network-level measures like *Nestedness* (*NODF: Nestedness Overlap and Decreasing Fill*), *connectance*, *generality* and *vulnerability*.

Nestedness: NODF gives the measure of nestedness (Almeida- Neto et al. 2008) with values from 0-100, higher values indicating higher nestedness. When species are ranked from most specialised to most generalised based on their interaction strength, a network is considered to be nested when specialist species (with lower number of mutualist partners) interact with subsets of the species with which generalist species (with higher number of mutualist partners) also interact (Mello et al., 2015) (refer Fig. 2a).

Connectance: Reflects the mean number of possible links (partners) per species of a network and is calculated as the sum of links divided by number of cells in the matrix. Eg. If there are four plants interacting with four birds in a network, there could be 16 possible links. If the observed links are just 4 out of the 16 possible links, connectance will be calculated as 0.25.

Generality: The mean number of plant partners per frugivore (García, 2016).

Vulnerability: The mean number of frugivore partners per plant (García, 2016).

The observed values of NODF and connectance were also compared with that of values derived from 1000 randomly generated networks (null-models) by constraining the marginal row and column totals to that of the observed network using the R-package bipartite (Dormann, Gruber, & Fründ, 2008). This was done to determine whether the observed networks were significantly different from the randomly generated ones.

Species-level

Species-level properties like *degree*, *betweenness centrality* and *closeness centrality* were also compared between contiguous and fragmented forests. The observed values of these metrics were compared between contiguous forests and fragments across different plant types (climbers, epiphytes, shrubs and trees) and for important plant families (Meliaceae, Moraceae, Myrtaceae, Rosaceae and Urticaceae). Similar comparisons were also done for small and large-bodied frugivores and important frugivore bird families like Bucerotidae (Hornbills), Columbidae (Pigeons), Rhamphastidae (Barbets), Pycnonotidae (Bulbuls), Sturnidae (Mynas), Chloropseidae (Leafbirds) and Oriolidae (Orioles). These comparisons were done to determine if certain species or families of birds play an important role in community organization. We also wanted to determine if birds belonging to a certain size class plays a more central role in the communities observed in the contiguous forests and in the fragments. Similarly, the comparisons were done to enquire if the observed network had certain species or plant families and their habits playing a key role in community organization.

Degree: Represents the number of mutualistic partners from the opposite trophic level for each species. Higher value represents more number of mutualistic partners.

Betweenness centrality: Measures how central is the position of the species in the network is, with a species having a high degree of interaction playing a more central role in the network.

Closeness centrality: Represents how close two species are from one another i.e. the smallest number of paths separating two species (Mello et al., 2015).

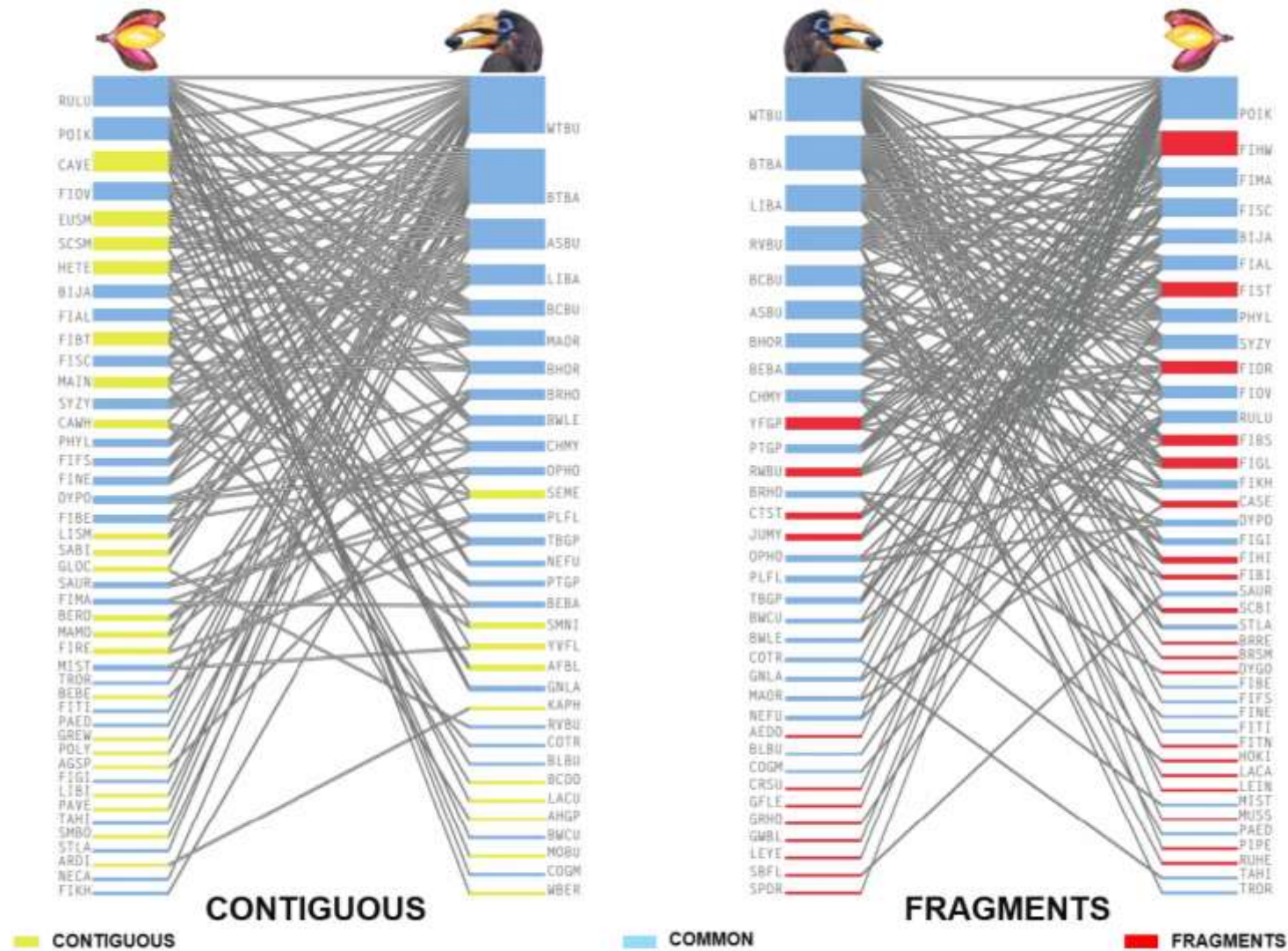


Figure 4: Unweighted plant-seed disperser networks of contiguous and fragmented forests. In each network, nodes on the left shows plant species and nodes on the right shows frugivore species; thickness represent the number of mutualist partners. The yellow nodes are species unique to the contiguous forests, blue nodes are common species and the red ones are the unique species to the fragments. Full bird and plant names associated with codes can be found in appendices.

RESULTS

Plant-disperser interactions

I documented a total of 592 interactions between 63 plant species and 44 avian frugivore species. Of the 63 plant species, 34 species were trees, 14 were climbers, 8 were epiphytes and 7 were shrubs.

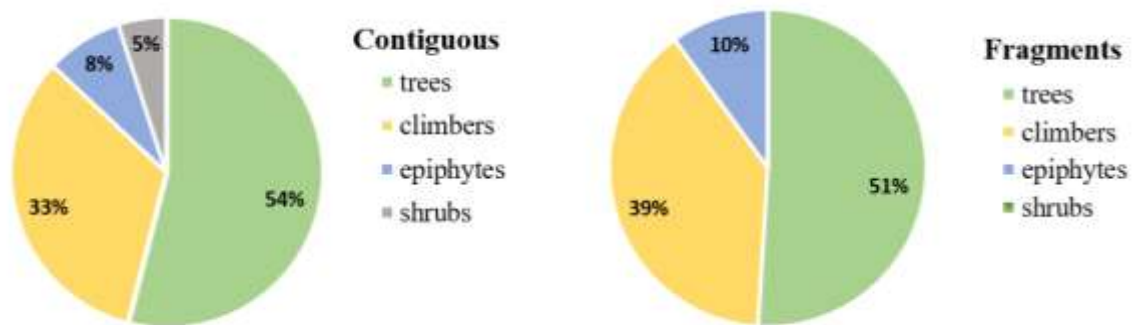


Figure 5: Percentage of total interactions observed on different plant habit types in contiguous and fragmented forests.

In contiguous forests, I documented 261 interactions between 44 plant species and 32 frugivore species (Fig. 5). While, in fragmented forest, I documented 328 interactions between 41 plant species and 34 frugivore species (Fig. 5).

A cluster of 12 different *Ficus* species constituted 27% of the total number of observed interactions in the contiguous forests. However, in fragments, a cluster of 17 different *Ficus* species alone had disproportionate contribution and constituted 51% of the total number of observed interactions (Fig. 6).

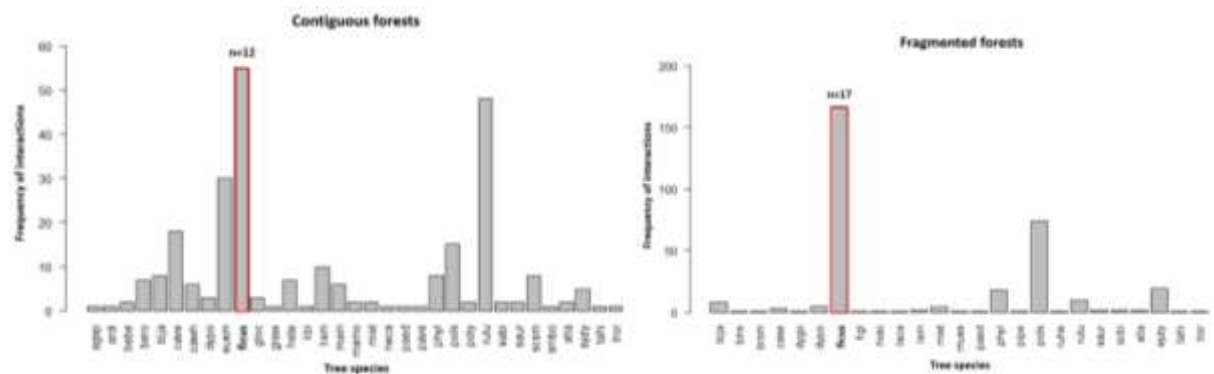


Figure 6: Frequency of observed interactions on tree species in contiguous forests (left) and fragments (right). All the ficus species (highlighted above) were merged to check their contribution from the total number of observed interactions.

Plants with short fruiting periods also made significant contribution to the total number of observed interactions during their fruiting peaks. Plants such as *Rubus lucens* (18%), *Eurya* sp. (11%) and *Callicarpa vestita* (7%) contributed significantly in contiguous forests while plants such as *Poikilospermum* sp. (22%), *Syzygium* sp. 6% and *Phyllanthus* sp. 6% contributed significantly to the total number of observed interactions in the fragments. There was 53% overlap of plants species and 65% overlap of frugivore species between contiguous and fragmented forests.

Network-level properties

The observed values of nestedness (NODF), connectance and links per species were lower in contiguous forests as compared to fragmented forests (Table 4). However, frugivores, had higher number of plant partners (generality) in the contiguous forest, while the plants had higher number of frugivore partners (vulnerability) in fragmented forests (Table 4).

Table 3: Network level properties of an unweighted network generated from the interactions observed in the contiguous forests and fragments.

Index	Contiguous	Fragment
NODF	30.465	35.739
Connectance	0.093	0.112
Links per species	1.724	2.080
Generality (Frugivore)	11.000	9.897
Vulnerability (Plants)	4.985	7.923

Depicted by the higher values of generality, frugivores fed on higher species of fruiting plants in the contiguous area. However, in the fragmented forests fruiting plants had more bird species feeding on them as depicted by the higher value of vulnerability (Table 4).

When the two observed networks were compared with 1000 randomly generated networks, I found that the observed networks were significantly more nested and connected as compared to null predictions (Table 5).

Table 4: Observed values and mean of the 1000 null model predictions of NODF and connectance.

Index	Treatment	Observed	Null mean	P-value
NODF	Contiguous	30.465	19.11	< 0.001
	Fragmented	35.739	21.90	< 0.001
Connectance	Contiguous	0.093	0.082	< 0.001
	Fragmented	0.112	0.095	< 0.001

Species-level properties

There was 51% (n = 63) overlap of plant species and 65% (n = 44) overlap of bird species between contiguous and fragmented forests. Eleven species of frugivores including Asian Fairy Bluebird, Ashy-headed Green Pigeon, Barred Cuckoo Dove and Mountain Bulbul were unique to the contiguous forests and 12 species of frugivores including Great Hornbill, Yellow-footed Green Pigeon, Jungle Myna, Chestnut-tailed Starling and Red-whiskered Bulbul were detected only in the fragmented forests. Three species of barbets (Blue-throated, Lineated and Blue-eared Barbet) and seven species of bulbuls (White-throated, Ashy, Black, Black-crested, Mountain (seen only in contiguous forests), Red-vented and Red-whiskered Bulbul (seen only in fragmented forests) contributed to 69% of the overall interactions in contiguous forests and 65% of the overall interactions in the fragmented forest.

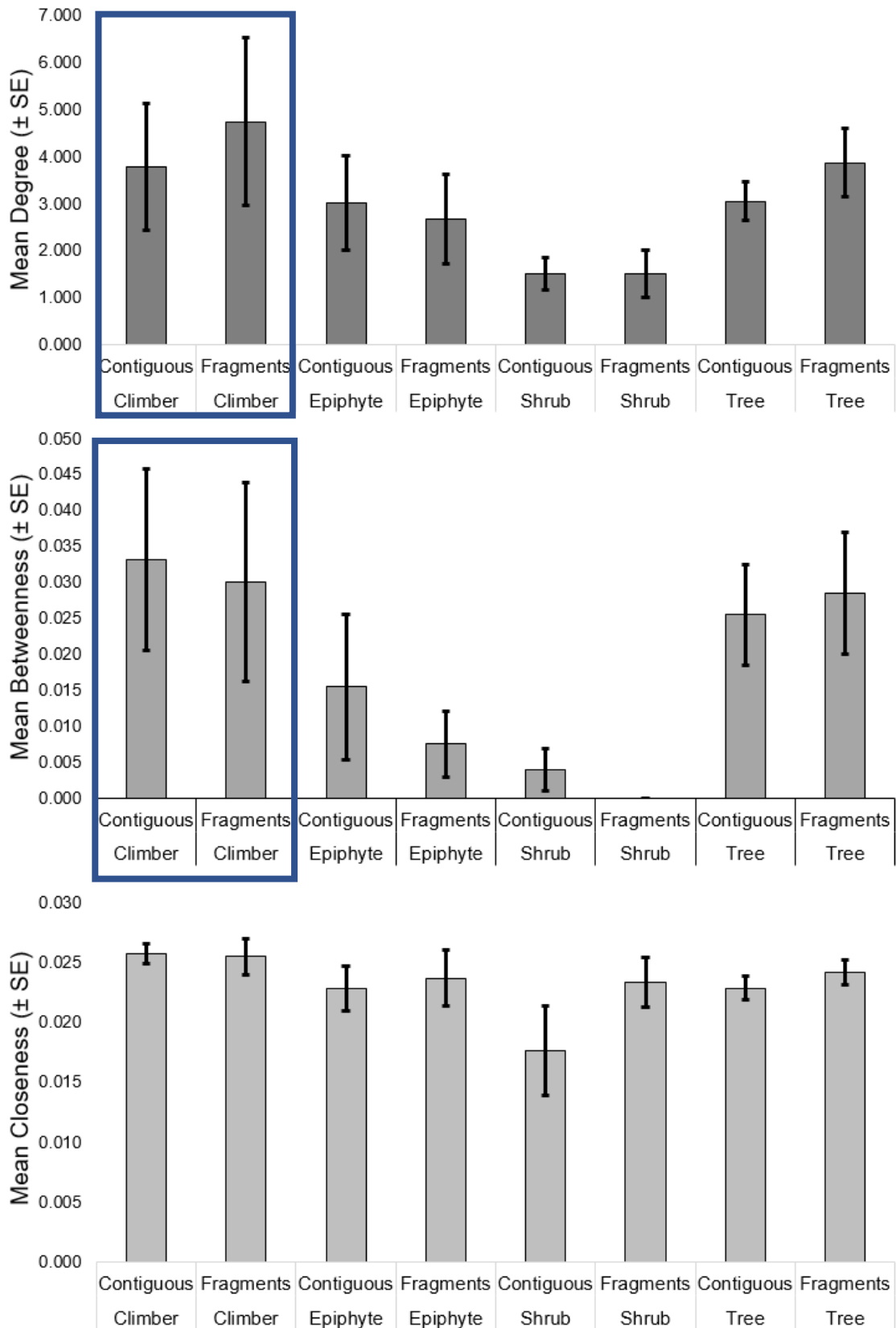


Figure 7: Mean (\pm SE) of Degree, Betweenness and Closeness across two habitat types for plant habits (climbers, epiphytes, shrubs and trees). Highlighted values depict higher values of degree and betweenness centrality for climbers compared to other plant forms.

Depicted by the higher values of mean degree, climbers were observed to have the highest mean number of frugivore partner species in both habitat types. However, marginally higher in the fragments, followed by trees, epiphytes and shrubs (Fig. 7). Climbers also had higher values of mean betweenness which makes climbers better connectors of different guilds in the community (Fig. 7).

Members of plant family Rosaceae and Urticaceae showed high values of mean Degree and Betweenness in fragments and contiguous forests. This pattern is driven because members of family Rosaceae and Urticaceae are both climbers and had the highest number of frugivore partner species in both habitat types. Family Rosaceae is represented by only one member species i.e. *Rubus lucens*, and family Urticaceae was represented by only one species that is *Poikilospermum* sp. Interestingly, *Poikilospermum* sp. had more frugivore partner species in fragments as compared to contiguous forests and the pattern was reversed for *Rubus* sp. (Fig. 8).

Although, members of family Moraceae (*ficus* spp.) contributed to the greatest number of total interactions observed, they were observed to have very few frugivore partner species compared to that of *rubus lucens* or *poikilospermum* sp (Fig. 8).

Members of family Meliaceae (large-seeded trees) were fed upon by unique frugivore species that ate only very few species of fruits indicated by lower closeness centrality values compared to other plant families (Fig. 8).

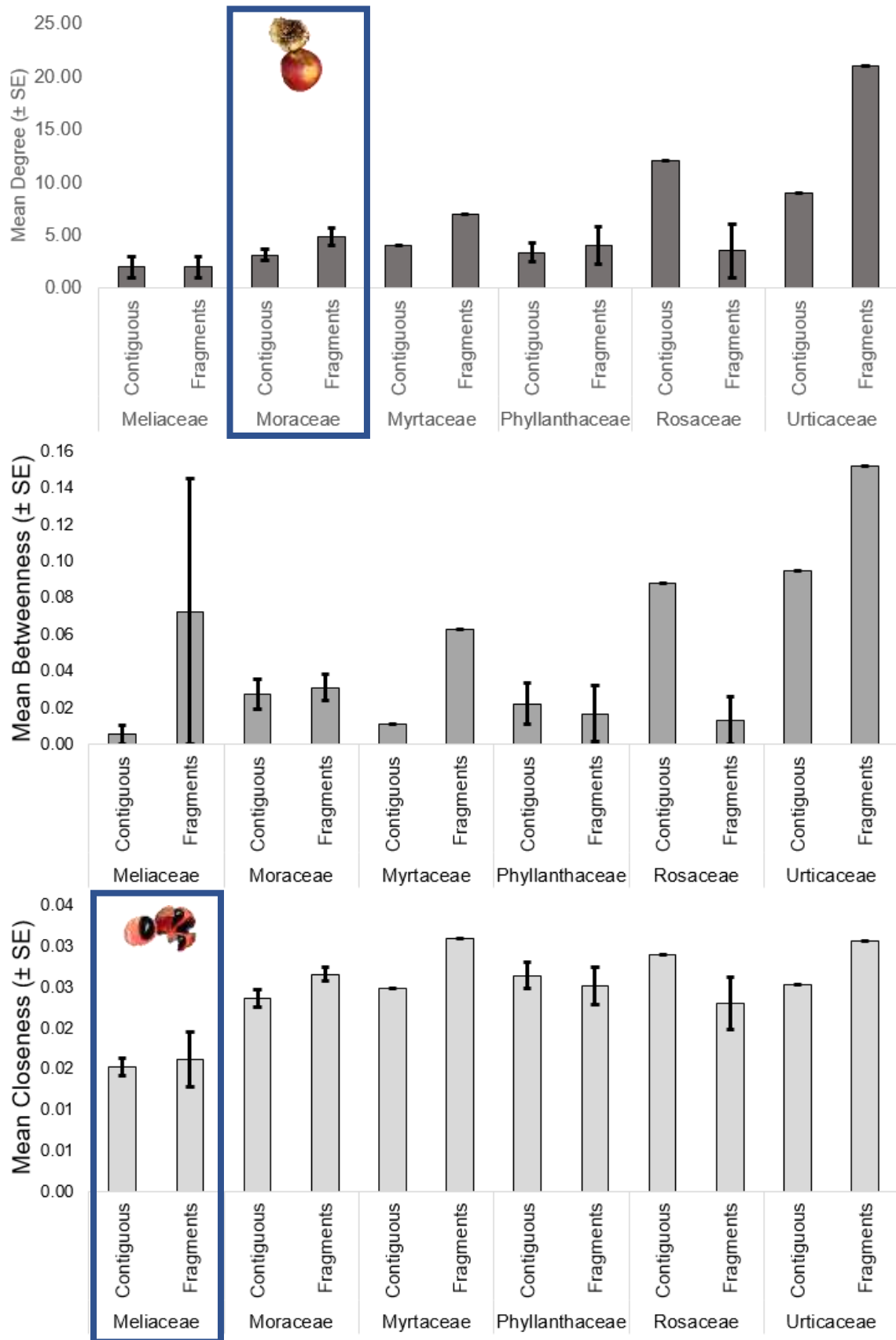


Figure 8: Degree, Betweenness and Closeness across two habitat types for frugivore family. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.

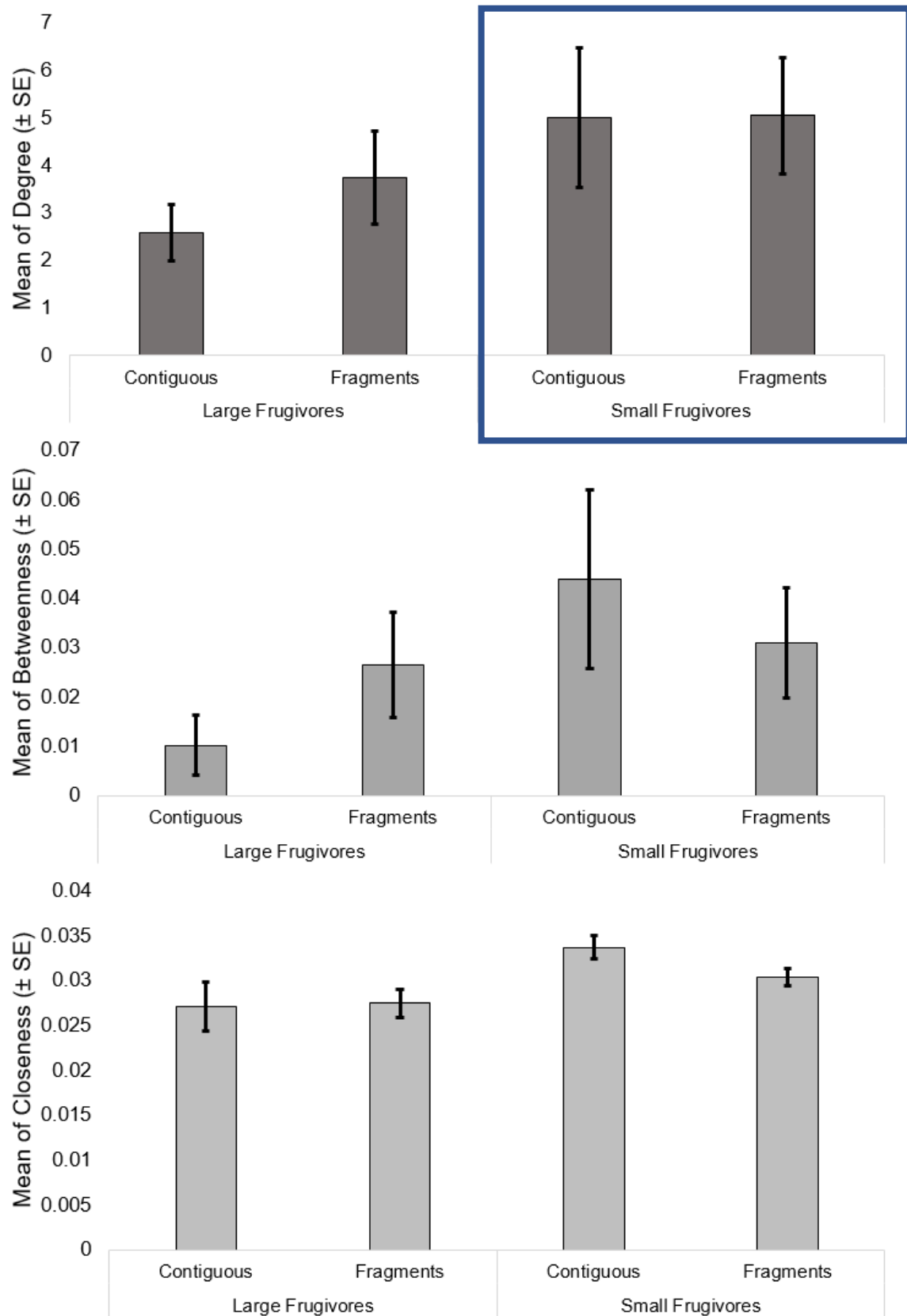


Figure 9: Degree, Betweenness and Closeness across two habitat types for large-and small-bodied frugivores. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.

65% of the observed frugivore species in both contiguous forests and fragmented forests were small-bodied. As also depicted by higher mean values of degree and betweenness, small frugivores were mostly generalist species, important connectors and fed on most available plant partner species. (Fig. 9).

Members of frugivore families Ramphastidae (Barbets) and Pycnonotidae (Bulbuls) had higher mean degree (mean number of plant partners) and mean betweenness as compared to other frugivore families in both contiguous and fragmented forests (Fig. 10). This pattern is driven because Bulbuls and Barbets constituted bulk of the total interactions are mostly also small-bodied frugivores.

Bucerotidae (Hornbills) had lower closeness centrality values which means they usually ate fruiting species that other birds couldn't eat (mostly the large-seeded ones). Hornbills fed on more unique fleshy-fruit species in the contiguous forests as compared to the fragments. This is depicted by higher mean values of degree and closeness in the contiguous forests (Fig. 10).

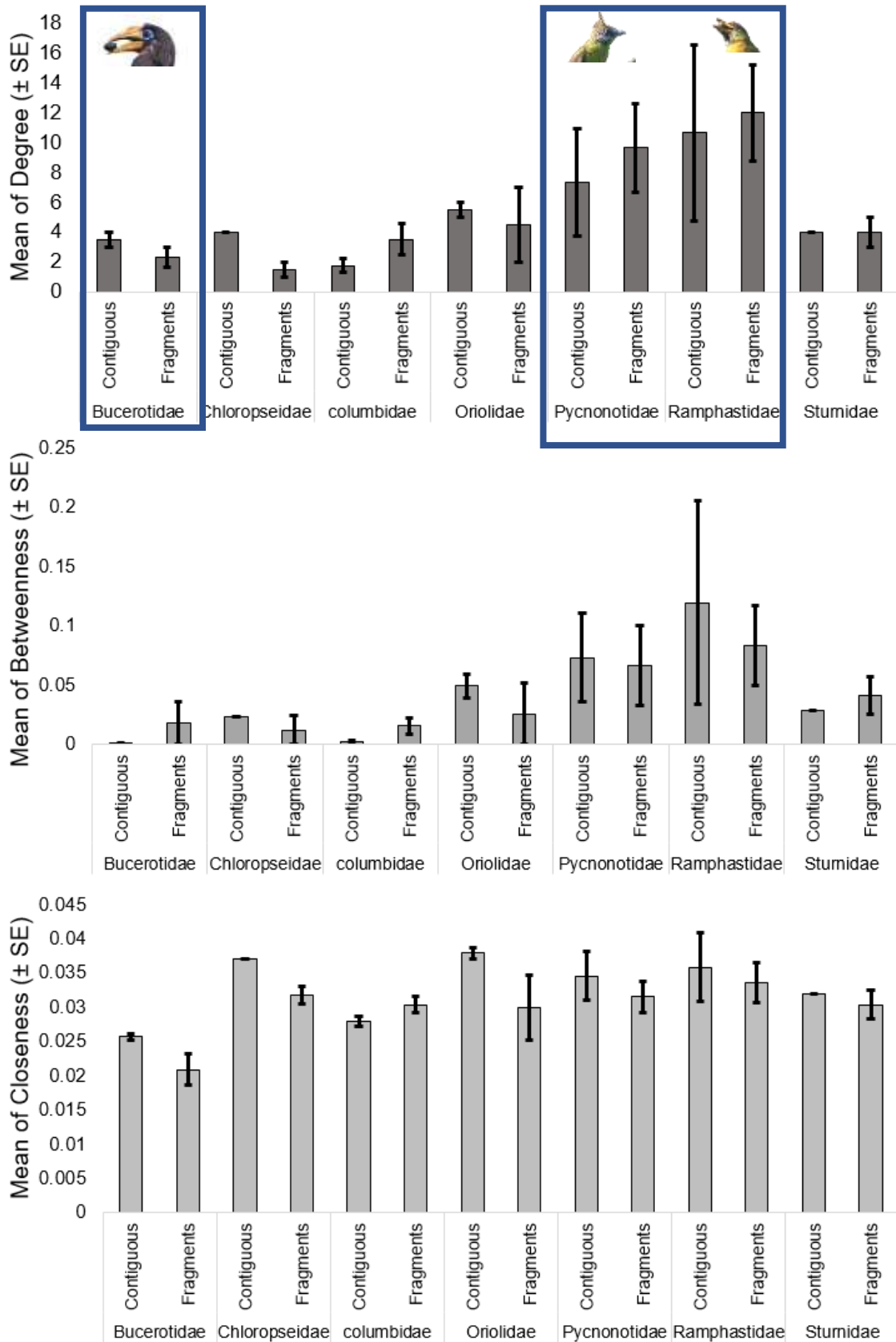


Figure 10: Degree, Betweenness and Closeness across two habitat types for frugivore family. The bars represent the mean and standard errors of species-level metrics in each network. Variation among species are denoted by the standard error bars.

DISCUSSION

This is the first study from India to compare organization of plant-bird disperser communities across contiguous and fragmented forests. The observed community of the contiguous forests was less nested, connected and had lesser links (partners) per species as compared to fragmented forests. While, the two networks were similar in terms of total number of mutualist species participating in the network organisation, there was a turnover of 47% plant species and 35% bird species in the fragments as compared to the contiguous forests. Climbers and epiphytes also come out as an important plant group in network organisation and more so in the fragments as compared to the contiguous forests. As pointed out by similar studies (Naniwadekar et al., 2019; Sankamethawee et al., 2011), intermediate frugivores like barbets and bulbuls and small-seeded fleshy fruits constituted bulk of total interactions and highlighting their key role in network organisation. Interestingly, contrary to several studies like Emer et al., 2018 and Kitamura et al., 2002 but in concurrence to Albrecht et al., 2014, our results suggest that large frugivores like hornbills were not lost in the fragments of our study system. We demonstrate the changes in network organisation of plant-seed disperser communities in fragments to that of the contiguous forests. This study highlights the conservation value of small reserves in maintaining functional connectivity through shared interactions.

Community-level patterns

Concurrent to the general trend, the observed network was more nested than randomly generated null networks (García, 2016) which could be because most specialist plants (with fewer frugivore partners) species also interact with the most generalist frugivores (with higher plant partners). The observed network was more nested and connected in fragments as compared to the network observed in the contiguous forest. Nestedness may be compromised in the contiguous forests because species may be forming distinct sub-communities of interacting species that interact much more with each other than to members of other sub-communities as has been reported elsewhere (Naniwadekar et al., 2019). The organization and composition of the communities into distinct sub-communities in fragments and continuous forests needs to be examined further to determine relatively lower values of nestedness in continuous forests. Evaluating the composition of communities in fragments and continuous forests will also allow an understanding of why plants have fewer partners in contiguous forests and frugivores have one partner more in contiguous forests. It will allow an understanding whether the observed patterns are driven by assemblage

which is unique to each of the two groups or whether there are dietary shifts happening in common species that is driving the observed patterns. The observed patterns of species-level properties such as generality and vulnerability may have implications for the observed nestedness and connectance levels at the community level.

Of plants, their habits and their role in structuring plant-disperser communities



Picture 1: Scandant climber of *Ficus sp.*

Climbers tended to interact with the greatest number of frugivores followed by epiphytes and trees. Both the contiguous and fragmented sites in my study area have had a history of logging and continue to experience logging pressures in varying intensities. Climber diversity and abundance has been reported to be higher in younger/degraded forests (Dewalt et al., 2000). Given the logging pressures and canopy openness in these logged areas, climbers seem to be playing an important role in structuring these communities. Our study sites showed really low values of basal area and stem density (Appendix 3, Page No. 35) when compared to unlogged forests in Arunachal Pradesh which shares boundaries with Lowland forests of Assam. The logged reserved forests of Arunachal Pradesh had basal area of 24 m² per ha, which was very close to the basal area values in our contiguous site. This suggests proliferation of climbers in our forests. (Naniwadekar et al., 2015)

It will be interesting to compare the relative role of climbers in structuring plant-disperser communities in unlogged and logged forests. Even in this dipterocarp-dominated forests, trees with fleshy fruits continue to play a key role in structuring plant-disperser communities as they were observed to have a higher number of mutualistic frugivore partners (high degree) and act as connector species (high betweenness) in species communities. On the other hand, shrubs had few partners and low degree and betweenness values as compared to other plant types indicating the relatively less important role they play in these communities. Climbers and epiphytes had larger mean number of partners in fragmented forests as compared to contiguous forests. The role of unique and common

species (to contiguous and fragmented forests) in driving this pattern needs to be examined further.

Among the different plant families, *Poikilospermum* sp. of the Urticaceae family had the highest diversity of frugivores visiting them in the fragments. This is indicated by greater value of mean degree and was evident since it associated with a greater number of unique frugivore partners including many insectivorous birds like Grey-winged Thrush, Lesser Yellowname, Spangled Drongo and non-forest generalist birds that are known to live in farmland edges like Red-whiskered Bulbul and Chestnut-tailed startling, Jungle Myna, etc.

In contiguous forests, climber *Poikilospermum* sp. was closely followed by another climber of Rosaceae family, *Rubus* sp. Both these climbers had high diversity of frugivores visiting them and are the key connector species in the logged contiguous forests and are likely driving the importance of climbers in these forests. Interestingly, the central role played by *Poikilospermum* sp. was more in fragmented forests as compared to contiguous forests but the pattern was inverse for *Rubus* sp. The important role played by Urticaceae members in forest edges and understorey has been acknowledged elsewhere (Vidal et al. 2013). Surprisingly, *Ficus* did not appear to play a more central role in these communities and had far fewer plant partner species as compared to *Poikilospermum* sp. and *Rubus* sp. and this pattern is in contrast to what has been reported elsewhere in north-east India (Naniwadekar et al. 2019). While *Ficus* dominated in the absolute number of interactions, they had a lower diversity of frugivores visiting them in general as compared to *Poikilospermum* sp. and *Rubus* sp. Large-seeded plant family like Myrtaceae had fewer but specialized partners as indicated by the low closeness centrality measures. Low closeness centrality value indicates that the species/group has specialized partners (Mello et al. 2015). *Syzygium* sp., which has medium-sized seeds (5-10 mm) and which belongs to the Myrtaceae family is an interesting species and it appears to have more specialized partners in contiguous forests as compared to fragmented forests where it has higher diversity of frugivores feeding on it, highlighting the role of *Syzygium* sp. as important tree members in tropical forest communities as has been indicated elsewhere (Naniwadekar et al., 2019). Higher diversity of frugivore partners for plants in forest edges due to influx of more open habitat species has been reported elsewhere (Menke et al., 2012)

Of bulbuls, barbets and hornbills



Picture 2: White-throated bulbul

Small frugivores and small-seeded plants constituted bulk of the total interactions. Many studies have pointed out that persistent interactions are largely performed by small-bodied frugivores and small-seeded plants in plant-frugivore networks (Palacio et al., 2016; Sankamethawee et al., 2011). They have also been reported to play a central role in maintaining functional connectivity and network cohesiveness as interactions between large-seeded plants and large bodied frugivores are naturally rare (Emer et al., 2018).

Barbets and bulbuls are among the key frugivores and seed dispersers in Asian tropics as has been highlighted in previous studies. (Naniwadekar et al., 2019; Sankamethawee et al., 2011). Given their small sizes they might be less-affected by habitat fragmentation and continue to be important dispersers in fragmented forests. Their wide dietary niche allows them to feed on a diverse array of plant species making them pivotal generalist seed dispersers for small- and medium-seeded plants. They are better connected than other important frugivore groups like the large-bodied hornbills and pigeons, mynas, leafbirds and orioles which have similar number of partners. With loss of large-bodied frugivores in fragmented habitats (Raman & Mudappa, 2003), small-bodied frugivores will play a crucial role in seed dispersal in these fragmented habitats.

Surprisingly, we detected hornbills and their interactions with fruiting plants in both continuous and fragmented forests. We detected Great and Brown Hornbills even in isolated fragments like Doomdooma Reserve. They were seen feeding on large-seeded plants like *Dysoxylum* spp. and *Horsfeildia kingii*, which have a smaller assemblage of seed dispersers. This explains the low closeness centrality values for hornbills which fed on unique species. This also indicates that hornbills are able to persist in fragments as small as 23 km² and play a key ecological role. While non-breeding home ranges of Great Hornbills are more than 50 km², breeding home ranges of Great Hornbills have been reported to be around 2 km² (Naniwadekar et al. unpublished data). I failed to detect Great Hornbills in contiguous forests, most likely as a consequence of high hunting pressures in

contiguous forest site which is adjacent to Arunachal Pradesh. Local *Nocte* communities in adjacent Arunachal Pradesh use the tail feathers of the Great Hornbills to adorn their headdresses and are known to frequent these contiguous forest sites to hunt (Rohit Naniwadekar pers. comm.). Hornbills are vulnerable to hunting pressures and have been reported to go locally extinct in Arunachal Pradesh (Naniwadekar et al., 2015). It is likely that they occur in extremely low densities in contiguous forests due to hunting pressures from neighbouring Arunachal Pradesh. Hornbills face hunting pressures even in these fragments, I witnessed a freshly killed Oriental Pied Hornbill which was shot with a catapult by a local villager. Given that they play a crucial role for large-seeded plants, loss of hornbills can have significant implications for large-seeded plant regeneration.

Interestingly, species that are found in less-abundant in forested areas (indicators of forest openness) like the Red-vented Bulbul was observed to be interacting with many more plant partners in the fragmented forest than it did in the contiguous forests. Similarly, Red-whiskered Bulbul was not at all detected in the contiguous forests, while they were prevalent seed dispersers in the fragments.

Way forward



Picture 3: Brown Hornbill's nest at its nest in a forest fragment.

Like other studies on plant-frugivore networks in a fragmented landscape (Emer et al., 2018) this study highlights that fragments can hold unique assemblages of plant-frugivore communities and may still maintain functional diversity of heterogenous forest landscape through shared plant-seed disperser interactions. Therefore, small reserves can make significant contribution in maintaining the diversity of plant-frugivore interactions which has important bearing for tropical forest regeneration and restoration of adjacent degraded areas. Understanding plant-seed disperser interactions to observe changes in the network organisation across two habitat types is a good way to find community level patterns and better understand the dynamics of species are organised in a community. Similar, studies must be carried out in more detail across all seasons and multiple years to get a holistic picture of impact of forest fragmentation on the plant-frugivore networks.

APPENDICES

Appendix 1: List of avian frugivore species that participated in the Network during the study period.

No	Common Name	Scientific Name	Code	Family	Body Mass	Size-Class
1	Asian Emerald Dove	<i>Chalcophaps indica</i>	AEDO	columbidae	136.54	Large
2	Asian Fairy-bluebird	<i>Irena puella</i>	AFBL	Irenidae	64.9	Small
3	Ashy-headed Green-Pigeon	<i>Treron phayrei</i>	AHGP	columbidae	234	Large
4	Ashy Bulbul	<i>Hemixos flavala</i>	ASBU	Pycnonotidae	32.5	Small
5	Black-crested Bulbul	<i>Rubigula flaviventris</i>	BCBU	Pycnonotidae	29.3	Small
6	Barred Cuckoo-dove	<i>Macropygia unchall</i>	BCDO	columbidae	168	Large
7	Blue-eared Barbet	<i>Psilopogon duvaucelii</i>	BEBA	Ramphastidae	33.3	Small
8	Black-hooded Oriole	<i>Oriolus xanthornus</i>	BHOR	Oriolidae	56.3	Small
9	Black Bulbul	<i>Hypsipetes leucocephalus</i>	BLBU	Pycnonotidae	51.8	Small
10	Brown Hornbill	<i>Anorrhinus austeni</i>	BRHO	Bucerotidae	1079.5	Large
11	Blue-throated Barbet	<i>Psilopogon asiaticus</i>	BTBA	Ramphastidae	90.5	Small
12	Black-winged Cuckooshrike	<i>Lalage melaschistos</i>	BWCU	Campephagidae	43	Small
13	Blue-winged Leafbird	<i>Chloropsis cochinchinensis</i>	BWLE	Chloropseidae	24.5	Small
14	Common Hill Myna	<i>Gracula religiosa</i>	CHMY	Sturnidae	192	Large
15	Common Green-Magpie	<i>Cissa chinensis</i>	COGM	Corvidae	126.64	Large
16	Collared Treepie	<i>Dendrocitta frontalis</i>	COTR	Corvidae	100.92	Large
17	Crimson Sunbird	<i>Aethopyga siparaja</i>	CRSU	Nectariniidae	6.7	Small
18	Chestnut-tailed Starling	<i>Sturnia malabarica</i>	CTST	Sturnidae	39.6	Small
19	Greater Necklaced Laughingthrush	<i>Ianthocincla pectoralis</i>	GNLA	Leiothrichidae	145.12	Large
20	Great Hornbill	<i>Buceros bicornis</i>	GRHO	Bucerotidae	2790.8	Large
21	Grey-winged Blackbird	<i>Turdus boulboul</i>	GWBL	Turdidae	97.1	Small

22	Golden-fronted Leafbird	<i>Chloropsis aurifrons</i>	GFLE	Chloropseidae	32.3	Small
23	Jungle Myna	<i>Acridotheres</i>	JUMY	Sturnidae	82.8	Small
24	Kalij Pheasant	<i>Lophura leucomelanos</i>	KAPH	Phasianidae	867.98	Large
25	Large Cuckooshrike	<i>Coracina macei</i>	LACU	Campephagidae	68	Small
26	Lineated Barbet	<i>Psilopogon lineatus</i>	LIBA	Ramphastidae	149	Large
27	Lesser Yellownappe	<i>Picus chlorolophus</i>	LEYE	Picidae	65.4	Small
28	Maroon Oriole	<i>Oriolus traillii</i>	MAOR	Oriolidae	73.7	Small
29	Mountain Bulbul	<i>Ixos mcclllandii</i>	MOBU	Pycnonotidae	32.5	Small
30	Nepal Fulvetta	<i>Alcippe nipalensis</i>	NEFU	Pellorneidae	15.8	Small
31	Oriental Pied-Hornbill	<i>Anthracoceros albirostris</i>	OPHO	Bucerotidae	892.9	Large
32	Plain Flowerpecker	<i>Dicaeum minullum</i>	PLFL	Dicaeidae	6.2	Small
33	Pin-tailed Pigeon	<i>Treron apicauda</i>	PTGP	columbidae	134.5	Large
34	Red-vented Bulbul	<i>Pycnonotus cafer</i>	RVBU	Pycnonotidae	42.9	Small
35	Red-whiskered Bulbul	<i>Pycnonotus jocosus</i>	RWBU	Pycnonotidae	29.5	Small
36	Scarlet-backed Flowerpecker	<i>Dicaeum cruentatum</i>	SBFL	Dicaeidae	5.6	Small
37	Silver-eared Mesia	<i>Leiothrix argentauris</i>	SEME	Leiothrichidae	28.4	Small
38	Small Niltava	<i>Niltava macgrigoriae</i>	SMNI	Muscicapidae	11.95	Small
39	Spangled Drongo	<i>Dicrurus hottentotus</i>	SPDR	Dicruridae	79.19	Small
40	Thick-billed Pigeon	<i>Treron curvirostra</i>	TBGP	columbidae	217.2	Large
41	White-bellied Erpornis	<i>Erpornis zantholeuca</i>	WBER	Vireonidae	11.8	Small
42	White-throated Bulbul	<i>Alophoixus flaveolus</i>	WTBU	Pycnonotidae	48.3	Small
43	Yellow-footed Green Pigeon	<i>Treron phoenicopterus</i>	YFGP	columbidae	235	Large
44	Yellow-vented Flowerpecker	<i>Dicaeum chrysorrheum</i>	YVFL	Dicaeidae	9	Small

Appendix 2: List of fruiting plant species that participated in the Network during the study period.

No	Scientific/Morpho name	Habit	Plant Code	Family	Seed-size
1	Aglaia spectabilis	Tree	AGSP	Meliaceae	Large
2	Ardisia sp.	Shrub	ARDI	Primulaceae	Medium
3	Beilschmiedia sp.1	Tree	BEBE	Lauraceae	Large
4	Beilschmiedia round	Tree	BERO	Lauraceae	Large
5	Bischofia javanica	Tree	BIJA	Phyllanthaceae	Medium
6	Bridelia red	Tree	BRRE	Phyllanthaceae	Medium
7	Bridelia small	Tree	BRSM	Phyllanthaceae	Small
8	Casearea sp	Tree	CASE	Lamiaceae	Medium
9	Callicarpa vestita	Tree	CAVE	Lamiaceae	Small
10	Callicarpa white	Shrub	CAWH	Lamiaceae	Small
11	Dysoxylum gotadhora	Tree	DYGO	Meliaceae	Large
12	Dysoxylum procera	Tree	DYPO	Meliaceae	Large
13	Eurya small	Tree	EUSM	Theaceae	Small
14	Ficus altissima	Tree	FIAL	Moraceae	Small
15	Ficus benjamina	Tree	FIBE	Moraceae	Small
16	Ficus bischofia	Tree	FIBI	Moraceae	Small
17	Ficus bigstalk	Tree	FIBS	Moraceae	Small
18	Ficus btmini	Tree	FIBT	Moraceae	Small
19	Ficus drupacea	Tree	FIDR	Moraceae	Small
20	Ficus fs	Tree	FIFS	Moraceae	Small
21	Ficus gibbon	Epiphyte	FIGI	Moraceae	Small
22	Figlike sp	Epiphyte	FIGL	Moraceae	Small
23	Ficus hirsute	Climber	FIHI	Moraceae	Small
24	Ficus highway	Tree	FIHW	Moraceae	Small
25	Ficus khokhon	Tree	FIKH	Moraceae	Small
26	Ficus maclellandii	Tree	FIMA	Moraceae	Small
27	Ficus nervosa	Tree	FINE	Moraceae	Small
28	Ficus oval	Epiphyte	FIOV	Moraceae	Small
29	Ficus repic	Epiphyte	FIRE	Moraceae	Small
30	Ficus scandens	Climber	FISC	Moraceae	Small
31	Ficus stalklong	Climber	FIST	Moraceae	Small

32	<i>Ficus tinctoria</i>	Epiphyte	FITI	Moraceae	Small
33	<i>Ficus tiny</i>	Epiphyte	FITN	Moraceae	Small
34	<i>Glochidion</i> sp	Tree	GLOC	Phyllanthaceae	Medium
35	<i>Grewia</i> sp	Shrub	GREW	Tiliaceae	Medium
36	<i>Heteropanax</i> sp	Tree	HETE	Araliaceae	Medium
37	<i>Horsfieldia kingii</i>	Tree	HOKI	Myristicaceae	Large
38	<i>Lantana camara</i>	Shrub	LACA	Verbenaceae	Small
39	<i>Leea indica</i>	Tree	LEIN	Vitaceae	Medium
40	<i>Litsea big</i>	Tree	LIBI	Lauraceae	Medium
41	<i>Litsea small</i>	Tree	LISM	Lauraceae	Medium
42	<i>Macaranga indica</i>	Tree	MAIN	Euphorbiaceae	Medium
43	<i>Magnolia montana</i>	Tree	MAMO	Magnoliaceae	Medium
44	<i>Mistletoe</i> sp	Epiphyte	MIST	Santalaceae	Small
45	<i>Mussaenda</i> sp	Climber	MUSS	Rubiaceae	Medium
46	<i>Neolamarckia cadamba</i>	Tree	NECA	Rubiaceae	Small
47	<i>Paederia</i> sp	Climber	PAED	Rubiaceae	Small
48	<i>Pavetta</i> sp	Shrub	PAVE	Rubiaceae	Medium
49	<i>Phyllanthus</i> sp	Climber	PHYL	Phyllanthaceae	Small
50	<i>Piper</i> sp	Climber	PIPE	Piperaceae	Small
51	<i>Poikilospermum</i> sp	Climber	POIK	Urticaceae	Small
52	<i>Polygonum</i> sp	Shrub	POLY	Polygonaceae	Small
53	<i>Rubus hexagynus</i>	Climber	RUHE	Rosaceae	Small
54	<i>Rubus lucens</i>	Climber	RULU	Rosaceae	Small
55	<i>Sabia</i> sp	Climber	SABI	Sabiaceae	Medium
56	<i>Saurauia</i> sp	Shrub	SAUR	Actinidiaceae	Small
57	<i>Schefflera big</i>	Tree	SCBI	Araliaceae	Medium
58	<i>Schefflera small</i>	Epiphyte	SCSM	Araliaceae	Medium
59	<i>Smilax borua</i>	Climber	SMBO	Smilacaceae	Medium
60	<i>Stephania lata</i>	Climber	STLA	Menispermaceae	Medium
61	<i>Syzygium</i> sp	Tree	SYZY	Myrtaceae	Medium
62	<i>Tapirai hirsuta</i>	Climber	TAHI	Connaraceae	Medium
63	<i>Trema orientalis</i>	Tree	TROR	Asteraceae	Small

Appendix 3: Attributes of vegetation of different study sites (Trail wise averages)

Place	Category/Fragment	Basal area (m²/ha)	Stem Density (per ha)	Mean Canopy (%)	Mean Height (m)
Bherjan	Small	21.76	728.30	37.34	9.91
Tokowoni	Small	23.04±0.95	818.71±553.11	45.22	9.25
Doomdooma	Medium	15.09±1.45	326.8±31.83	32.10	9.17
Kakojan	Medium	51.49±24.22	952.13±418.04	49.67	10.61
Jeypore	Contiguous	35.04±14.02	803.3±318.41	50.00	12.62
Soraipong	Contiguous	18.17	672.46	47.97	9.73

REFERENCES

- Achard, F., Beuchle, R., Mayaux, P., Stibig, H. J., Bodart, C., Brink, A., ... Lupi, A. (2014). Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology*, 20(20), 2540–2554. <https://doi.org/10.1111/gcb.12605>
- Albrecht, J., Gertrud Berens, D., Jaroszewicz, B., Selva, N., Brandl, R., & Farwig, N. (2014). Correlated loss of ecosystem services in coupled mutualistic networks. *Nature Communications*, 5(May), 1–8. <https://doi.org/10.1038/ncomms4810>
- Champion, S. H., & Seth, S. K. (1968). *A revised survey of the forest types of India*. Government of India Press, Nasik.
- Chen, Q., Tomlinson, K. W., Cao, L., & Wang, B. (2017). Effects of fragmentation on the seed predation and dispersal by rodents differ among species with different seed size. *Integrative Zoology*, 12(6), 468–476. <https://doi.org/10.1111/1749-4877.12273>
- Cox, G. W. (2002). *General ecology laboratory manual*. Brown Publishers.
- Cramer, J. M., Mesquita, R. C. G., & Bruce Williamson, G. (2007). Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, 137(3), 415–423. <https://doi.org/10.1016/j.biocon.2007.02.019>
- Davidar, P., & Morton, E. S. (1986). The Relationship Between Fruit Crop Sizes and Fruit Removal Rates by Birds. *Ecology*, 67(1), 262–265.
- Dewalt, S. J., Schnitzer, S. A., & Denslow, J. S. (2000). Density and Diversity of Lianas along a Chronosequence in a Central Panamanian Lowland Forest. *Journal of Tropical Ecology*, 16(1), 1–19.
- Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite Package : Analysing Ecological Networks. *R News*, 8(October), 8–11.
- Emer, C., Galetti, M., Pizo, M. A., Guimarães, P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. *Ecology Letters*, 21(4), 484–493. <https://doi.org/10.1111/ele.12909>
- Estrada, A., & Fleming, T. H. (1986). *Frugivores and seed dispersal*. (A. Estrada & T. H. Fleming, Eds.). Dr. W Junk Publishers.

- Fleming, T. H., Randall, B., & Whitesides, G. H. (1987). Patterns of Tropical Vertebrate Frugivore Diversity. *Annual Review of Ecology and Systematics*, 18, 91–109.
- Freeman, L. C., & Mulholland, R. (1979). Centrality in Social Networks. *Journal of Theoretical Biology*, 2, 119–141.
- García, D. (2016). Birds in Ecological Networks: Insights from Bird-Plant Mutualistic Interactions. *Ardeola*, 63(1), 151–180. <https://doi.org/10.13157/arla.63.1.2016.rp7>
- Hagen, M., Kissling, W. D., Rasmussen, C., Aguiar, M. A. M. De, Brown, L. E., Carstensen, D. W., ... Olesen, J. M. (2012). *Biodiversity, Species Interactions and Ecological Networks in a Fragmented World. Global Change in Multispecies Systems* (1st ed., Vol. 46). Elsevier Ltd. <https://doi.org/10.1016/B978-0-12-396992-7.00002-2>
- Janzen, D. H. (1970). Herbivores and the Number of Tree Species in Tropical Forests. *The American Naturalist*, 104(940), 501–528. <https://doi.org/10.1086/282687>
- Jordano, P. (1995). Angiosperm Fleshy Fruits and Seed Dispersers: A Comparative Analysis of Adaptation and Constraints in Plant-Animal Interactions. *The American Naturalist*. <https://doi.org/10.1086/285735>
- Jordano, P. (2000). Fruits and frugivory. *Seeds: The Ecology of Regeneration in Plant Communities*, 125–165. <https://doi.org/10.1079/9780851994321.0125>
- Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant properties in coevolutionary network of plant-animal interactions. *Ecology Letters*, 6, 69–81.
- Jordano, P., Forget, P., Lambert, J. E., Böhning-gaese, K., Traveset, A., Wright, S. J., ... Bo, K. (2010). Frugivores and seed dispersal : mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, 7(November 2010), 321–323. <https://doi.org/10.1098/rsbl.2010.0986>
- Kakati, K., Chelam, R., Qureshi, Q., & Gupta, A. . (2005). Impact of Forest Fragmentation on the Hoolock Gibbon (*Hylobates hoolock*) in Assam (India), (October), 218.
- Kanjilal, U., & Das, A. (n.d.). *Flora of Assam*. Omsons Publications, New Delhi.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., & Noma, N. (2002). Interactions between Fleshy Fruits and Frugivores in a Tropical

- Seasonal Forest in Thailand. *Oecologia*, 133(4), 559–572.
- Laurance H. E. M.; Laurance, S. G.; Andrade, A. C.; Fearnside, P. M.; Ribeiro, J. E. L.; Capretz, R. L., W. F. . N. (2006). Rain forest fragmentation and the proliferation of successional trees TT - Rain forest fragmentation and the proliferation of successional trees, 87(2), 469–482. <https://doi.org/10.1890/05-0064>
- Lenz, J., Böhning-gaese, K., Fiedler, W., & Mueller, T. (2015). Nomadism and seasonal range expansion in a large frugivorous bird. *Ecography*, 38, 54–62. <https://doi.org/10.1111/ecog.00522>
- Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., & Wright, S. J. (2012). Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals, 26(6), 1072–1081. <https://doi.org/10.1111/j.1523-1739.2012.01927.x>
- Mello, M. A. R., Rodrigues, F. A., Costa, L. da F., Kissling, W. D., Şekercioğlu, Ç. H., Marquitti, F. M. D., & Kalko, E. K. V. (2015). Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos*, 124(8), 1031–1039. <https://doi.org/10.1111/oik.01613>
- Menke, S., Böhning-Gaese, K., & Schleuning, M. (2012). Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. *Oikos*, 121(10), 1553–1566. <https://doi.org/10.1111/j.1600-0706.2011.20210.x>
- Mitchell, K. (2010). Quantitative Analysis by the Point-Centered Quarter Method. Retrieved from <http://arxiv.org/abs/1010.3303>
- Naniwadekar, R., Chaplod, S., Datta, A., Rathore, A., & Sridhar, H. (2019). Large frugivores matter: insights from network and seed dispersal effectiveness approaches. *Journal of Animal Ecology*, (March), 1–13. <https://doi.org/10.1111/1365-2656.13005>
- Naniwadekar, R., Mishra, C., & Datta, A. (2015). Fruit resource tracking by hornbill species at multiple scales in a tropical forest in India. *Journal of Tropical Ecology*, 31(6), 477–490. <https://doi.org/10.1017/S0266467415000449>
- Naniwadekar, R., Mishra, C., Isvaran, K., Madhusudan, M. D., & Datta, A. (2015).

- Looking beyond parks: the conservation value of unprotected areas for hornbills in Arunachal Pradesh, Eastern Himalaya. *Oryx*, 49(2), 303–311.
<https://doi.org/10.1017/s0030605313000781>
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, 104(50), 19891–19896. <https://doi.org/10.1073/pnas.0706375104>
- Osuri, A. M., Chakravarthy, D., Mudappa, D., Raman, T. R. S., Ayyappan, N., Muthuramkumar, S., & Parthasarathy, N. (2017). Successional status, seed dispersal mode and overstorey species influence tree regeneration in tropical rain-forest fragments in Western Ghats, India. *Journal of Tropical Ecology*, 33(4), 270–284.
- Palacio, R. D., Valderrama-Ardila, C., & Kattan, G. H. (2016). Generalist Species Have a Central Role In a Highly Diverse Plant – Frugivore Network. *Biotropica*, 43(3), 349–355. <https://doi.org/10.1111/btp.12290>
- Raman, T. R. S., & Mudappa, D. (2003). Correlates of hornbill distribution and abundance in rainforest fragments in the southern Western Ghats, India. *Bird Conservation International*, 13(3), 199–212.
<https://doi.org/10.1017/s0959270903003162>
- Rocha-Santos, L., Pessoa, M. S., Cassano, C. R., Talora, D. C., Orihuela, R. L. L., Mariano-Neto, E., ... Cazetta, E. (2016). The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. *Biological Conservation*, 196(April 2016), 1–9. <https://doi.org/10.1016/j.biocon.2016.01.028>
- Sankamethawee, W., Pierce, A. J., Gale, G. A., & Hardesty, B. D. (2011). Plant-frugivore interactions in an intact tropical forest in north-east Thailand. *Integrative Zoology*, 6(3), 195–212. <https://doi.org/10.1111/j.1749-4877.2011.00244.x>
- Schleuning, M.; Blüthgen, N.; Flörchinger, M.; Braun, J.; Schaefer, M. H. & Böhning-gaese, K. (2011). Specialization and interaction strength in a tropical plant — frugivore network differ among forest strata. *Ecology*, 92(1), 26–36.
<https://doi.org/10.1890/09-1842.1>
- Schleuning, M., Böhning-Gaese, K., Dehling, D. M., & Burns, K. C. (2014). At a loss for birds: Insularity increases asymmetry in seed-dispersal networks. *Global Ecology*

- and *Biogeography*, 23(4), 385–394. <https://doi.org/10.1111/geb.12134>
- Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, 21(8), 464–471. <https://doi.org/10.1016/j.tree.2006.05.007>
- Shanahan, M., & Compton, S. G. (2001). Vertical Stratification of Figs and Fig-Eaters in a Bornean Lowland Rain Forest : How Is the Canopy Different ? Author (s): Mike Shanahan and Stephen G . Compton Reviewed work (s): Vertical stratification of figs and fig-eaters forest : how is the can, 153(1).
- Shanahan, M., Samson, S. O., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: A global review. *Biological Reviews of the Cambridge Philosophical Society*, 76(4), 529–572.
- Sharma, N., & Sinha, A. (n.d.). Narayan Sharma Anindya Sinha. *Encounter*.
- Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., ... Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences*, 112(24), 7472–7477.
- Terborgh, J. (1992). Maintenance of Diversity in Tropical Forests. *Biotropica*, 24(2), 283–292.
- Vidal, M. M., Hasui, E., Pizo, M. A., Tamashiro, J. Y., Silva, W. R., & Guimarães, P. R. (2014). Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*, 95(12), 3440–3447.
- Wilman, H., J., B., J., S., C., de L. R., M., R., & W, J. (2014). EltonTraits 1 . 0 : Species-level foraging attributes of the world ' s birds and mammals. *Ecology*, 95(October 2013), 2027.
- Wotton, D. M., & Kelly, D. (2011). Frugivore loss limits recruitment of large-seeded trees. *Proceedings of the Royal Society B: Biological Sciences*, 278(1723), 3345–3354.
- Wright, S. J. (2002). Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia*, 130(1), 1–14.