OPEN TO INVASION? PATTERNS IN FRUITING PHENOLOGY AND SEED DISPERSAL OF *LANTANA CAMARA* ACROSS DIFFERENT HABITATS IN NORTH INDIA

Dissertation submitted to the

Saurashtra University, Rajkot-360005, Gujarat

In partial fulfilment of

Master's Degree in Wildlife Science

By

YUKTI TANEJA

Under the Supervision of

Dr. NAVENDU PAGE

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

December, 2021

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DECLARATION

I, **Yukti Taneja**, hereby declare that the research work titled **"Open to Invasion? Patterns in fruiting phenology and seed dispersal of *Lantana camara* across different habitats in north India"**, carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Dr. Navendu Page, Dr. R. Suresh Kumar** of the Wildlife Institute of India and **Dr. Rohit Naniwadekar** of Nature Conservation Foundation from August 2021 to December 2021. I hereby declare that this work has not been submitted for any other degree of any university.

Date: December 25, 2021

Place: Dehradun

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Azadi Ka Amrit Mahotsav

CERTIFICATE

This is to certify that Yukti Taneja has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science of the Saurashtra University, Rajkot, Gujarat. The topic of her dissertation is "**Open to Invasion? Patterns in fruiting phenology and seed dispersal of *Lantana camara* across different habitats in north India**". The study was carried out under our supervision from August 2021 to December 2021. We hereby certify that this work has not been submitted for any degree to any university.

Dr. Navendu Page
Supervisor

Dr. R. Suresh Kumar
Co-supervisor

Dr. Rohit Naniwadekar
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CERTIFICATE OF PLAGIARISM CHECK

It is certified that the M.Sc. dissertation titled **"Open to Invasion? Patterns in fruiting phenology and seed dispersal of *Lantana camara* across different habitats in north India"** submitted by Ms. Yukti Taneja has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) regulations. The following inferences are drawn from this check:

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ACKNOWLEDGEMENT

This thesis is the documentation of not just a scientific endeavour but a very personal journey of learning to endure uncertainty of the oddest kinds. Yet, persisting only to seek the experience that is research in Ecology. This would not have been possible without an army of people who were around to support at different stages, topics and field sites that the masters dissertation bestowed me with.

I would first like to thank my family back home, who have been the pillars of strength, even when it was nearly impossible from all fronts, for us to keep at it. I thank them for putting quite an unflinching faith and pride in me while supporting me financially for doing a course that they had never even heard of!

I thank Dr. Jhala for teaching me innumerable and precious lessons through MSc. But, most importantly for the lesson to never leave hands of 'hope', that good health and a good scientific work doesn't have to come at the cost of each other. I am forever grateful for his scolding, support and exhibition of courage to extend guidance for both the serious and the silliest problems.

This dissertation would not been possible without the enthusiasm of my supervisors. Dr. Navendu Page, Dr. R. Suresh Kumar and Dr. Rohit Naniwadekar. I am deeply grateful to Rohit for keeping faith in this work and me even on the days when nobody else could have possibly seen this through. He has been around to cheer up and check on me, in a manner that it helped me in not just keeping at it, but learning to enjoy it. His loudest acts of care and conviction has made I and this thesis work. I am most thankful to him for guiding the design of the field sampling of the study such that it was practically an ode to 'one day at a time', because that was all I could do. His enthusiasm and teachings on life and science has been crucial, not just in studying but also on acting like a seed. I hope many more students discover him because he sure will continue to be the human hornbill dispersing the 'seeds' that are his students, 'in and at' the best conditions for them to germinate. I sincerely thank Navendu, for being the most diligent listener that I know of. It is hard to make him believe but he has been one of the most successful teachers to I and my batch mates, for instilling the love for plants in us. His careful questioning on my very unstructured thoughts and writings have helped me understand the most basic questions, which always challenged and improved my understanding of this study. I look forward to learn more about the lives of plants, possibly only because of the way Navendu has taught us to look and appreciate them (but also to not sound like a plant noob and to never embarrass him for being our teacher!). I thank Suresh sir for his time and patience during the study and for carefully examining understanding of the study. I thank him for helping in arranging logistical support and advice.

I thank our course directors Dr. Samrat Mondol and Dr. Navendu Page for being very patient and keen in solving through the difficulties that the pandemic bestowed on this course. I thank them for being there in the best of their capacity to talk through and guide us whenever we needed their support. I thank Negi Ji for all his care and time in making every day in WII so much better and welcoming for us. I thank the WII support staff for keeping the institute and its goals for biodiversity conservation functional by doing their duties with utmost dedication.

I sincerely thank the Forest Department, Uttarakhand for providing me the permits to conduct this study. I thank Director, Dean and Faculty of WII for their giving their time and inputs to this course.

I thank Dr. Sutirtha Dutta and Dr. Qamar Qureshi for being sounding boards of encouragement and advice and Dr. Abhijit Das for bringing joy to our days in WII. I am grateful to Rishad Naoroji for being an inspiration for where I started my thesis. I thank Kavita Isvaran, Ajith Sir, Anand Osuri, Monika Kaushik for encouraging discussions at different stages of the master's dissertation. I thank the researchers of WII for depicting the fortitude in persisting at their research in difficult times. I am all gratitude to Aashna Sharma, Ninad Mungi and Bipin CM for their carefully crafted advice on ecology and life. I cannot thank Aashna enough for being the consistent cheerleader and for putting her unflinching faith in me through the past year. I thank Aaranya Gayathri for being the senior I didn't know I needed. I am indebted to Varun Kher, Rajat Rastogi and Arpitha Jayanth for responding to all the panic texts and calls, for lending their ears on all the silly things that scared me, and always putting me back on right track.

I thank Dr. Jahnavi Joshi for her prompt help with the phylogenetic tree. I thank Rintu Mandal for his very generous help and troubleshooting in the HMSC analysis and Sameeha Pathan for her help with spatial analysis that would not have been possible in the short time without them. I thank Abdus Shakur, Akshita Kaushik, Sipu Kumar and Rounak Patra for their help in days of fieldwork. I also thank Vignesh Chandran and Shakur for patiently helping me understand bird calls better. I sincerely thank Harish Bhatt for his assistance on field and his enthusiasm in conducting this study.

I am all gratitude to all my XVII batchmates, for being such fierce and resilient bunch of wildlife fanatics to keep at things even in the hardest of times. If I could only change one thing about this thesis, it would be to have submitted and celebrated it with them, for I have very dearly missed them around every day of my extended stay at WII.

I thank Manu for being an indispensable part of the everyday adventures and learnings at WII. I am grateful to him for sharing his stories, laughter and care in enriching my experiences here. I thank Joonu and Patel for being consistent company in dancing and snacking through the unforeseen challenges of MSc. I thank Divya and Anubhuti, for inspiring with their exhibit of sheer resilience in fieldwork that we started together. I thank Ashish for choosing to stay, witness and talk through on some crushing turning points of this thesis. I thank Tarun for being the most candid and funniest company throughout the journey. I thank Jithin for lending his ears and sharing experiences in troubleshooting both, excel and mental health.

I thank the Kite runners in Delhi, for introducing me to Ecology and the everyday challenges it brings. I thank them for the legacy to keep grounded, to treat both successes and failures as imposters and to never underestimate the potential of the ecological laboratories that is our backyards.

I have saved the last and very important bit to mention people who have been the *hafiz* of support and encouragement in the most 'intangible' ways. I thank Dr. Hari Sridhar for passing on from his seniors, as he called it the "generosity with their time" through conversations with him that I have most looked forward to, in the inbox or at the end of a week. He has added to my personal recovery and academic decisions in ways that cannot possibly be tracked with particular events and words. He has been the reason for many things that worked out, and for the many days that I persisted at it. I thank my brother, Deepak Taneja for being the giant on whose shoulders I continue to stand and experience the luxury of taking risks and opportunities. I thank Mrigya Kaushik, Garima and Manvi Pant for being consistent cheerleaders from the days when I sold seed pencils for conservation

I very humbly acknowledge my own spirit to have started from the very scratch, over and again through the past year. Yet, never losing on my excitement for the science of ecology in the face of the lot of life that happened quite 'alongside' it.

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SUMMARY

Lantana camara (hereafter, *Lantana*) is a fleshy-fruited alien invasive plant that spreads mainly through seed dispersal mediated by vertebrate frugivores. *Lantana* has low shade tolerance and is thus more abundant in relatively open habitats. While open habitats may facilitate better germination of seeds and growth of saplings and adults, the role of habitat type on its reproductive output (fruits) and seed dispersal remains largely unknown. Understanding this can help predict differential patterns of invasion in different habitats. In this study, I aimed to understand the influence of canopy cover and other drivers on fruiting phenology, visitation patterns of frugivores on *Lantana* and fruit removal of *Lantana*.

I carried out this study in *Shorea robusta*-dominated moist deciduous forest and grassland-shrubland mosaics in and around the Wildlife Institute of India (WII) campus in the Dehradun valley, Uttarakhand from August 2021 to December 2021. To determine the influence of canopy cover on fruiting phenology, I marked and monitored (every fortnight) 45 *Lantana* bushes across a gradient of canopy cover from late August. To determine the drivers of visitation patterns of frugivores on *Lantana* and the fruit removal rates of *Lantana* across habitats, I carried out focal plant watch on 80 *Lantana* bushes across a gradient of canopy cover. I used a generalized linear mixed model (GLMM) to test the effect of canopy cover and shrub volume on the fruit crop size of *Lantana* bushes monitored for phenology.

I used Non-metric Multidimensional Scaling (NMDS) to examine if the frugivore assemblage of *Lantana* differed between the open and closed habitats. To determine species-level responses of frugivores to focal shrub and habitat covariates, I used Hierarchical Model of Species communities (HMSC) framework. I identified the most effective seed dispersers of *Lantana* from visitation rates and fruit handling behaviour using Seed Dispersal Effectiveness (SDE) landscape. I used a generalized linear model to identify the factors determining the visitation rates of the effective seed disperses on *Lantana*.

I found that *Lantana* shrubs that had lower canopy cover over them had significantly higher ripe fruit crop sizes than shrubs that had high canopy cover. Frugivore assemblage visiting *Lantana* differed marginally between open and closed habitats. While the visitation of Bulbuls on *Lantana* was negatively influenced by canopy cover, visitation of Indian White-eye was positively influenced by surrounding shrub cover. Red-vented Bulbul, Himalayan Bulbul and Indian White-eye were the most effective seed dispersers of *Lantana.* Visitation rates of the most effective dispersers on *Lantana* was negatively affected by canopy cover indicating that shrubs with lower canopy cover over them had higher visitation rates of seed dispersers than shrubs with higher canopy cover.

This study highlights the importance of canopy cover in driving fruiting and seed dispersal of *Lantana.* Thus, this study provides evidence for higher fruiting and seed dispersal as a potential mechanism that can lead to higher invasion of *Lantana* in relatively open habitats through higher propagule pressure. Additionally, findings of this study also imply that disturbances like lopping that creates canopy openings and gaps in the forests are likely to result in higher fruiting and seed dispersal of *Lantana* facilitating its invasion in the forests.

INTRODUCTION

Invasion by alien plant species is a leading threat to the persistence of native biodiversity (Pyšek et al., 2012; Vilà et al., 2011). Invasive plants outcompete native plants thereby reducing the recruitment of native plant species (Hejda et al., 2009; Pyšek et al., 2012; Sundaram and Hiremath, 2012). Through rapid invasion, these species can change forest structure (Asner et al., 2008). Since invasive species may differ in the leaf-area index, transpiration rates and root depth, they alter hydrological cycles (Calder and Dye, 2001; Le Maitre et al., 2015). They alter carbon and soil nutrient cycling affecting ecosystem productivity (Liao et al., 2008; Weidenhamer and Callaway, 2009). They can increase the propensity of fires with a positive feedback loop leading to further invasion and degradation of habitats (Brooks et al., 2004; Hiremath and Sundaram, 2005). Thus, invasive species can have widespread impacts ranging from species to ecosystems (Clavero and García-Berthou, 2005; Miniat et al., 2021; Mollot et al., 2017; Traveset and Richardson, 2006). The spread of invasive species is facilitated by high propagule pressure and suitable abiotic conditions (e.g. increased light conditions or disturbance) (Charbonneau and Fahrig, 2004; Lockwood et al., 2005). Many invasive plant species are typically open habitat species and thus canopy cover or gap sizes are suggested to play an important role in their spread (Charbonneau and Fahrig, 2004).

Several alien invasive plant species are fleshy-fruited. These species are often characterised by small seed sizes and large fruit crop sizes (Gosper and Vivian-Smith, 2009). Small-seeded plants can be effectively dispersed by a diverse array of frugivores (Naniwadekar et al., 2019). Frugivores track fruiting trees with large fruit crops (Gopal et al., 2020; Naniwadekar et al., 2015). Thus, advertisement of such fruit traits, aids in opportunities for easier acquisition of mutualistic frugivore partners facilitating their invasion through seed dispersal (Buckley et al., 2006; Gosper and Vivian-Smith, 2010; Jordaan et al., 2011).

Such is the case of *Lantana camara,* a fleshy-fruited invasive plant that has spread widely in tropical forests worldwide (Bhagwat et al., 2012; Mungi et al., 2020; Sharma et al., 2005). *Lantana* has severe deleterious effects on the abundance, distribution, richness and population structure of native plant species in diverse habitats (Gooden et al., 2009; Kumar et al., 2020; Sundaram and Hiremath, 2012). Owing to its limited shade tolerance, it grows best in unshaded habitats (Duggin and Gentle, 1998). Nevertheless, it can invade forests via forest edges and forest gaps created due to disturbances like logging (GISD, 2021). The impact of *Lantana* on the native community structure of plants varied among forest habitat types (Sundaram and Hiremath, 2012). However, the impact was consistently higher for scrub-savanna deciduous forests than evergreen forest, possibly owing to canopy openness and disturbance. Given that *Lantana* prefers open habitats, habitat features (e.g. canopy cover) may also influence the reproductive output (fruit crop size of plants). L*antana* reproduces sexually and asexually (Sharma et al., 2005), and has sugar-rich, small-seeded fruits (Bitani et al., 2020; Embaby and Mokhtar, 2011). These fleshy fruits are fed upon by a diverse assemblage of frugivores, especially birds (Aruna and

Balasubramanian, 2017; Ramaswami et al., 2017, 2016; Turner and Downey, 2008). The gut treatment of seeds enhance germination success and reduce the germination times of *Lantana* (Jordaan et al., 2011). Most of the studies have been carried out in a single habitat but *Lantana* fruiting and seed dispersal rates may vary across habitat types.

The fruiting pattern will influence the number of seeds available for dispersal and seed dispersal rates will determine the number of seeds dispersed in the landscape. Both these aspects are critical for the invasion of *Lantana*. Additionally, the disperser assemblage of *Lantana* can also vary across habitats. The foraging decisions of seed dispersers may also be driven by preferences for different habitat features that increases safety (García et al., 2011; Martínez and García, 2015). This may have important implications for the invasion of *Lantana* in different habitats. This aspect has been poorly explored in the literature.

Studying the variation in patterns of fruiting and seed dispersal of invasive species like *Lantana* across habitats can provide information on the potential mechanisms influencing the invasion of alien species. Further, it can also help in predict the invasibility of habitats, which can guide in devising strategies for the management of invasion (Alpert et al., 2000). Thus, for this study, I aimed to understand the problem of *Lantana* invasion across different habitats by focusing on their fruiting and fruit removal (Traveset and Richardson, 2006).

To this end, I asked the following specific questions: 1) How does the fruiting phenology of *Lantana* change across habitats varying in canopy cover? 2) Does frugivore assemblage of *Lantana* vary across the habitats? 3) How do frugivore species respond to habitat and focal shrub characteristics? 4) Which frugivore species are the most effective seed dispersers of *Lantana*? 4) What habitat and focal bush characteristics influences visitation rate of the effective seed dispersers on *Lantana*?

METHODS

Study area

This study was conducted in and around the Wildlife Institute of India (WII) campus (30.282°N, 77.974°E) in the Dehradun city, Uttarakhand, India (Figure 1). The average temperature in the study area varies from 10.8°C to 27.9°C annually. The average annual rainfall is 1441 mm (https://en.climate-data.org/). The major land-use types around the WII campus include built-up areas, agricultural fields and fallow lands, Sal (*Shorea robusta*) dominated by moist-deciduous forest and a mosaic of grasslands and shrublands. To the north of the WII campus is a mix of agricultural fields and built-up area and to the east is mostly built-up area (Figure 1). A narrow strip of built-up area and fields separates the forest patch of WII from the *S. robusta* dominated moist deciduous forests of the Asarori Range of the Dehradun Forest Division. While the WII campus harbours regenerating moist deciduous patches (~20 years old) of *S. robusta* (Family: Dipterocarpaceae), the Asarori range harbours tall, dominant stands of *S. robusta*. Commonly seen associates of these Sal forests are *Mallotus philippensis*, *Terminalia elliptica*, *Clerodendrum infortunatum*, *Murraya koenigii*, *Ardisia solanacea*, *Colebrookea oppositifolia* and *Flemingia semialata*. Grassland-shubland mosaics are characterised by grass species like *Phragmites karka* and *Chrysopogon zizanoides*, and woody species like *Broussonetia papyrifera*, *Celtis tetrandra*, *Syzygium cumini*, *Triadica sebifera*, *Ziziphus mauritiana*, *Carissa spinarum*, *Pyrus pashia and Flueggea virosa. Lantana* is among the most dominant shrubs in the forest and open habitats (Mandal and Joshi, 2014).

The frugivore community consists of generalist frugivores like Red-vented Bulbul *Pycnonotus cafer*, Himalayan Bulbul *Pycnonotus leucogenys*, Red-whiskered Bulbul *Pycnonotus jocosus*, Asian Pied Starling *Gracupica contra*, Brown-headed Barbet *Psilopogon zeylanicus*, Indian White-eye *Zosterops palpebrosus* as well as specialist frugivores including Oriental Pied Hornbill *Anthracoceros albirostris* and Indian Grey Hornbill *Ocyceros birostris.* In the forest, the major anthropogenic disturbances are cattle grazing along the forest edges and the fireline, and lopping of *Terminalia elliptica* for providing fodder to the cattle (Appendix 7).

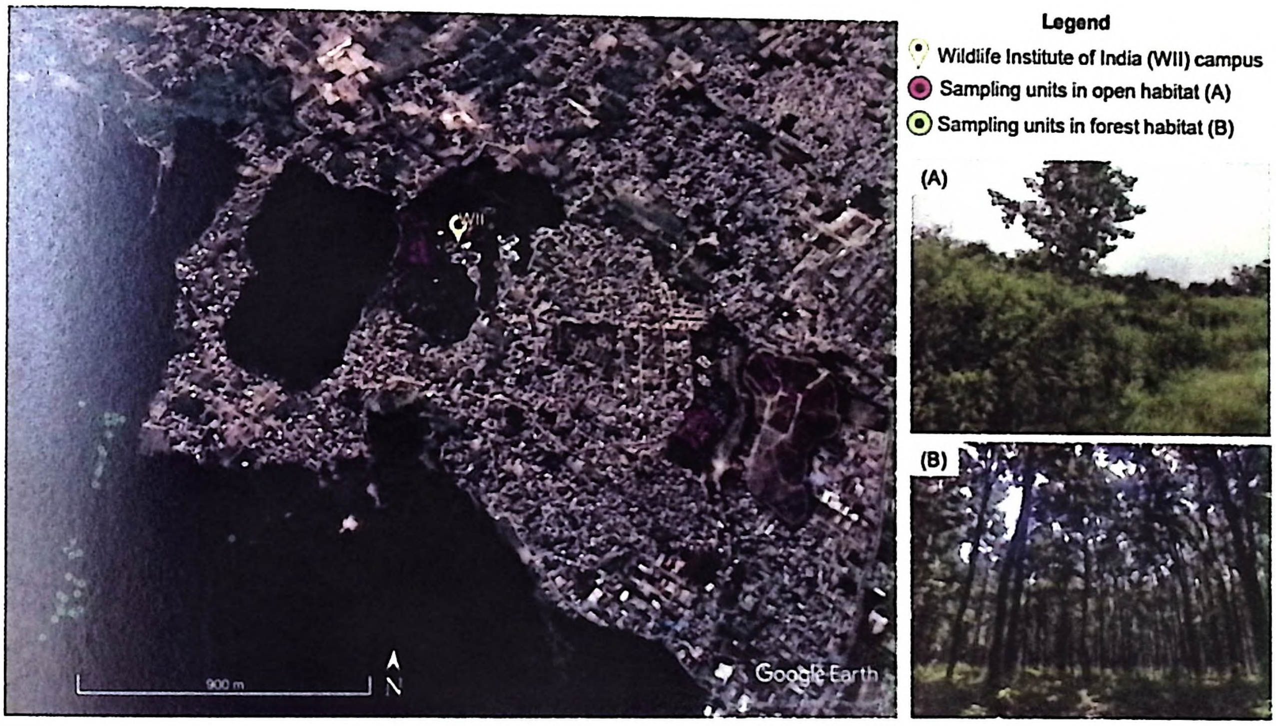

Figure 1. Map showing the sampling units around the WII campus. Sampling units are shown as points in green for Sal-dominated forest habitat and in pink for three sites in the grassland-shrubland mosaics i.e. the open habitat. See methods for additional details.

Study species

Lantana camara L., a thorny shrub native to the South and Central America is considered as one of the world's ten worst invasive alien species (Ghisalberti, 2000; Richardson and Rejmánek, 2011). Its rapid range invasion of tropical habitats worldwide is an urgent problem in conservation science (Bhagwat et al., 2012; Mungi et al., 2020). Evidence suggests that *Lantana* has a potential of posing a great threat to wildlife habitats as well as native flora (Aravind et al., 2010; Gooden et al., 2009; Sundaram and Hiremath, 2012). *Lantana* is a fleshy-fruited plant that can produce over 100,000 small purple-black berries in a single season, presenting an abundant and attractive food resource for the frugivores (Ramaswami et al., 2017). Generalist species, like Bulbuls, are known to disperse their seeds at long distances (Sharma et al., 2005). *Lantana* also spreads vegetatively through root suckers.

Fruiting phenology of *Lantana* across different habitats

A total of 45 *Lantana* bushes, 15 bushes each in forest interior, forest edges, and grassland-shrubland mosaic (Appendix 4),were marked opportunistically in August 2021 and monitored every fortnight till November 2021. During each monitoring session, I recorded the number of ripe and unripe fruits on the focal bush (Appendix 5). Only bushes taller than 1m were marked to avoid sampling younger plants. The minimum distance between the bushes was at least 20 m. For every focal phenology bush, I also estimated the shrub volume and canopy cover above the bush. For estimating shrub volume, I measured diameter of the bush at right angles (A and B) and the height (H) of the bush crown and used the formula $2/3 \times \pi \times H \times (A/2 \times B/2)$

following Thorne et al., (2002). I estimated the canopy cover at four points along the edge of the bush using the mobile application CanopyApp (https://posters.unh.edu/gallery/view/2605/).

Frugivore assemblage of *Lantana* across different habitats

I conducted focal watches on 80 *Lantana* bushes using established methods (Ramaswami et al. 2017). To get variation in canopy cover and to ensure a balanced design, I sampled 40 bushes each in forest and grassland-scrubland mosaic habitats. The focal tree watches were conducted between September to November 2021 which coincided with the peak fruiting of *Lantana* (see Figure 2). Each focal bush was observed only once. One to two observers watched each focal *Lantana* bush for a duration of three hours either in the morning (between 0625 to 1020 hr) or afternoon (between 1325 to 1800 hr) using Nikon 8×42 binocular. The observers sat at least 8-10 m away from the focal plant using the existing shrubs as cover so as to minimise the influence of observer on the frugivore visitations. Bushes were consecutively watched in open and closed habitats. Bushes that were watched on the same day in a single habitat were selected at least 80 m apart and were observed after an interval of at least three hours. The mean and median distances among focal *Lantana* shrubs for each site is given in Appendix 6.

During each focal tree watch, I recorded all the visitors on *Lantana* and only those, which were observed handling fruits were classified as frugivores. I recorded the species identity, number of individuals and arrival and departure times of all the visitors. In addition, I conducted focal scans of individual frugivores to document the fruit handling behaviour (the number of fruits swallowed, pecked, dropped and carried away) of the visitors following established methods (Naniwadekar et al., 2019).

Habitat and focal shrub characteristics

Since the visitation of frugivores on *Lantana* bush could be influenced by ripe fruit crop size, fruiting neighbourhood, bush characteristics (shape and size) and the habitat in the immediate vicinity of the bush, I recorded the following parameters immediately after the focal watch of the *Lantana* bush. This data was collected for all the 80 focal bushes that were observed.

Ripe fruit crop size: *Lantana* berries are borne in clusters on a common stalk. Before every focal watch, I counted the number of ripe fruits on the focal bush. For most bushes (~90%), I counted the absolute number of ripe fruits on the plant. When the bush was too large or dense making it difficult for total counts, I counted fruits in one portion of the bush and extrapolated for the entire bush following established methods (Ramaswami et al., 2017).

Fruiting neighbourhood: Since frugivore visits can be influenced by fruit availability in the neighbourhood of the fruiting plant (Guerra et al., 2017), ripe fruit crop size of conspecific and hetero-specific fruiting plants were counted for plants within 5m radius from the centre of the focal *Lantana* bush.

Shrub volume: The size of the shrub could influence the frugivore visit. Therefore, I estimated shrub volume. I considered the shrub as an ellipse, and I measured the longest axis of the shrub (A), the axis perpendicular to A (B), and the height of the shrub (H). The shrub volume was calculated using the following formula $2/3 \times \pi \times H \times (A/2 \times B/2)$ (Thorne et al., 2002). Occasionally the *Lantana* shrub has a thin long stem that shoots up from the main vegetative part of the bush. To avoid overestimation of the volume, I did not consider of the height of the tallest stem but considered the height of the majority of the vegetative part of the bush, excluding the single tall stem that emerged from the main bush.

Habitat: In the scrub thorn forests of Mudumalai, the visitation of the White-browed Bulbul *Pycnonotus luteolus* was influenced by the habitat around the focal fruiting shrub and not the fruit availability on or in the neighbourhood of the focal plant (Jayanth, 2020). Therefore, I estimated tree density, tree height, basal area, canopy cover, shrub cover, grass or herb cover and cover height around each of the focal bush to determine the influence of habitat characteristics on visitation patterns of frugivores (Appendix 1)

I enumerated and measured the girth of all woody plants with GBH $\geq$30 cm (girth at breast height) within 10m radius from the centre of the focal bush after the focal tree watch to estimate tree density and basal area. The basal area of each tree was calculated using the following formula: $(GBH)^2/4\pi$ and summed for all trees within a plot. I measured the height (using a Hawke LRF 400 range finder) of each tree. Canopy cover was estimated at the edge of each focal shrub in four cardinal directions using the Android application called 'CanopyApp' that has been specifically developed by the University of New Hampshire for measuring canopy cover (https://posters.unh.edu/gallery/view/2605/). The four values were averaged to estimate the mean percentage canopy cover over the focal fruiting shrub.

All woody vegetation within 10 m radius around the focal fruiting bush (excluding trees ≥30 cm GBH) was considered as shrub cover. I expected that such vegetation provides escape cover to the frugivores. I visually estimated the shrub and grass/herb cover within 10 m from the centre of the focal fruiting shrub around the focal shrub. The percentage shrub and grass/herb cover was estimated by visually dividing the 10m radius plot into four parts and calculating percentage cover for one quarter at a time. The sum of the four values gave the estimate of the total shrub and grass/her cover for the plot. Cover height was measured by walking three steps (~3m) in six cardinal directions from the edge of focal bush, and recording the height of the vegetation using a measuring tape.

Data analysis

Drivers of fruiting in *Lantana*

Data from the 45 shrubs that were periodically monitored was used for this analysis. I wanted to test for the influence of canopy cover on ripe fruit crop availability. The ripe fruit crop on the bush could also be influenced by shrub volume and the timing of the monitoring session. Therefore, I tested the influence of canopy cover and shrub volume using the Generalized Linear Mixed Model (GLMM) with a negative binomial error distribution using the package 'glmmTMB' (since the count data was overdispersed). The predictors was standardised prior to analysis to determine the relative influence of each variable on fruit crop size of the shrub. Since I had monitored each shrub every 15 days across seven sessions, I used monitoring session as the random effect in the model (since the relationship between response and predictor variables could vary across different monitoring sessions). The marginal R^2 (variation explained by fixed effects only) and conditional R^2 (variation explained by fixed and random effects) were used to assess model fit.

Frugivore composition of *Lantana* across open and closed habitats

For this analysis, I used data from the 80 fruiting bushes that were observed for frugivore visitations. To examine the variation in frugivore species composition visiting the focal *Lantana* shrubs across the habitat type, I used non-metric multidimensional scaling (NMDS) along two axes with Bray-Curtis dissimilarity metric from the R package 'vegan' (Oksanen et al., 2020). Since the bushes were broadly selected in open (grassland-shrubland mosaic) and closed forests (*Shorea* dominated forests), I compared frugivore visitation across open and closed forests. The difference in frugivore community composition between two habitats were statistically tested using the 'anosim' (Analysis of similarities) function in 'vegan'. The observed value was compared with a null distribution (number of permutations = 999). The *R* statistic, which is the proportion of mean dissimilarity between the groups to mean dissimilarity within the groups, was used to determine the differences across the two categories.

Factors influencing frugivore visits on *Lantana*

To determine the factors that influence visitation patterns of different frugivores on *Lantana,* I used the Hierarchical Model of Species communities (Ovaskainen and Abrego, 2020) approach. HMSC is a joint species distribution model (Warton et al., 2015) which includes a hierarchical layer asking how species responds to environmental variables and how this response depends on the species traits and phylogenetic relationships.

For this analysis, I used the focal *Lantana* bushes (n = 80) as sampling units. As HMSC doesn't model the distribution of very rare species, I excluded the frugivore species that visited less than five focal *Lantana* bushes, which left us with seven species including Cinereous Tit *Parus cinerous*, Grey-breasted Prinia *Prinia hodgsonii*, Himalayan Bulbul, Indian White-eye, Red-vented Bulbul, Red-whiskered Bulbul and Yellow-eyed Babbler *Chrysomma sinense*. I modelled the presence-absence of these seven species as a function of canopy cover, tree density, shrub cover, cover height, fruit crop size, fruiting neighbourhood and bush volume.

Species traits used in the analysis included beak length (till the culmen), beak width and hand-wing index. These traits correspond to the ability of the bird to feed on fruits (beak length and width) and dispersal (hand-wing index). The data for species traits were acquired from comprehensive functional trait data database "Avonet" (Tobias et al., 2021). I acquired time-calibrated Phylogenetic tree for the species of interest using https://birdtree.org/ (Jetz et al., 2012). I fitted the HMSC model with the R-package Hmsc (Tikhonov et al., 2020) assuming the default prior distributions (following Ovaskainen and Abrego, 2020). I sampled posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each of which was run for 37,50,000 iterations, of which the first 12,60,000 were removed as burn-in. The chains were thinned by 10,000 to yield 250 posterior samples per chain. I examined MCMC convergence by examining the potential scale reduction factors (Gelman and Rubin, 1992) of the model parameters. I examined explanatory power of the data of the model using the Tjur's R^2 values (Tjur, 2009). Only if the 95% credible intervals on the estimated coefficients for each of the predictor did not overlap zero, we interpreted the predictor to significantly influence the probability of visitation of the frugivore species on fruiting *Lantana* shrub. I also examined if phylogenetically closely-related species responded similarly- to understand if the niches of the frugivore species were structured phylogenetically.

Effective seed dispersers of *Lantana*

To determine the effective seed dispersers of *Lantana*, I used the 'Seed Dispersal Effectiveness Landscape' with associated effectiveness isoclines by plotting the mean visitation rate (per hour) on the x-axis and the proportion of fruits swallowed on the y-axis following Schupp et al. (2010) and Jordano (2014). For this, I considered all the frugivores which were seen swallowing the fruits of the *Lantana* during my study or reported as seed dispersers in other studies (Ramaswami et al., 2017, 2016).

Determinants of overall seed disperser visits to *Lantana*

The Seed Dispersal Effectiveness identified the most effective seed dispersers of *Lantana*. I determined the drivers of the combined encounters of the most effective dispersers of *Lantana* using Generalized Linear models (GLM) fitted with a negative binomial error distribution using the package MASS (Venables and Ripley, 2002 since the data was overdispersed). I tested the effect of habitat (canopy cover, tree density, shrub cover, cover height) and focal shrub characteristics (shrub volume and fruit crop size) on the number of effective seed dispersers that visited *Lantana*. The predictor variables were standardised to determine the relative influence of the different predictor variables.

I checked for collinearity by determining correlation among the predictor variables for the GLMM and GLM analysis using the Spearman's correlation test. The correlations between the predictor variables were ≤ 0.7. Since I expected that the set of predictors used in the model would influence the response variable, I used the global model. Model fit was assessed using McFadden's pseudo R^2. Model coefficients with 95% confidence intervals that did not overlap zero were considered to have an effect over the number of visitations of effective seed dispersers.

RESULTS

Lantana was observed to be fruiting in both the open (grassland-shrubland mosaic) and closed (sal-dominated moist deciduous forests) habitats throughout the study period. I recorded 451 individual visits of 14 avian frugivore species on 80 *Lantana* bushes. From the total 451 visits, 320 visits comprising 12 species, were recorded in open habitat (n=40), while 131 visits were from nine species in forest habitat (n=40). The three most frequent frugivore visitors in open habitat were Red-Vented Bulbul (103 visits) followed by Himalayan Bulbul (76 visits) and Indian White-eye (53 visits). In the Forest Habitat, the most frequent visitors were Indian White-eye (48 visits), Grey-breasted Prinia (40 visits) and Himalayan Bulbul (21 visits). Out of the 14 frugivore species, 11 were considered as seed dispersers as they were observed to swallow fruits as shown in the Appendix 2. A total of 21 (~50%) focal *Lantana* bushes in the closed habitat got at least one frugivore visit. Whereas, 36 (~90%) focal bushes in Open habitat got at least one frugivore visit. Other than avian frugivores, I also opportunistically observed troop of Rhesus Macaque (*Macaca mulatta*) swallowing *Lantana* fruits in the WII campus and Sal Forest.

Patterns in fruiting phenology of *Lantana*

Lantana was fruiting in both open and forest habitats but, the quantum of fruits were much higher in open (grassland-shrubland) habitat (Figure 2). I also observed the temporal variation in fruit crops of *Lantana* across the sampling period (Figure 2). The temporal trends suggested that the peak fruiting of grassland-shrub habitats as well as the forest edge (fire line) habitats occurred around late September to early October. Whereas, in the forest interior, a smaller peak occurred in late October. The results from GLMM showed that the number of ripe fruits on the *Lantana* bush was negatively affected by canopy cover i.e. *Lantana* shrubs in closed forests had smaller fruit crops than those in the open habitats (Table 1; Figure 3). Larger *Lantana* shrubs has larger fruit crops but the slope coefficients for bush volume was smaller than canopy cover indicating stronger influence of canopy cover than bush volume in influencing fruit crops (Table 1).

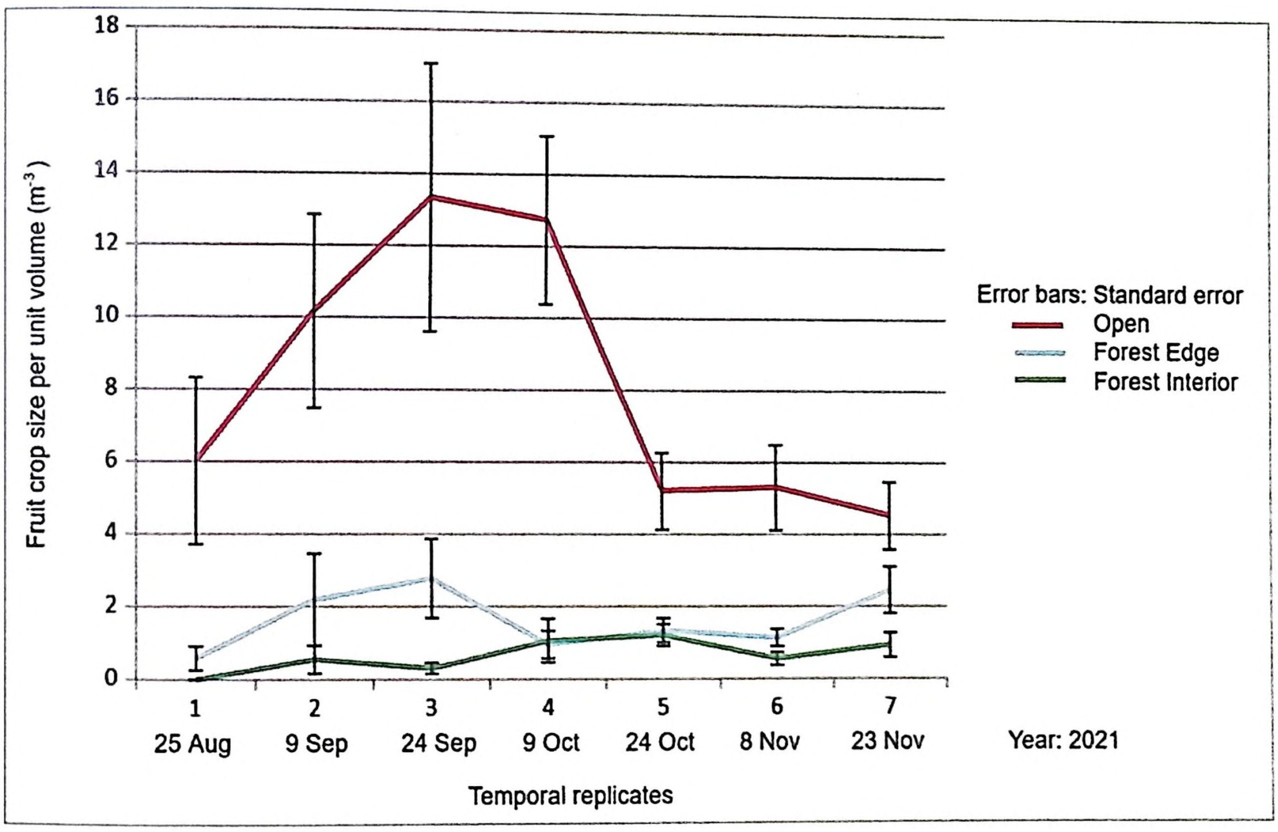

Figure 2. Temporal variation in fruiting among habitat types. The x-axis shows temporal sessions of phenology monitoring every 15 days starting 25 August, 2021. The y-axis represents the fruit crop size (number of ripe fruits on the focal *Lantana* bush) controlled for bush volume.

Table 1. GLMM coefficients and their 95% confidence intervals for testing the relationship between fruit crop size with shrub volume, canopy cover and temporal replicate. Parameter coefficient(s) with 95% CIs not overlapping zero have been highlighted in bold. The marginal (R^2_m) and conditional R^2 (R^2_c) for the models have also been reported.

Response variable		**Predictor variable (scaled)**	**Estimate (95% CI)**	R^2_m	R^2_c
Number of ripe fruits on the bush. (Fruit crop size)	Fixed effects	**(Intercept)**	**2.66 (2.31 – 3.0)**	0.77	0.87
		Canopy cover	**-1.06 (-1.27 – -0.85)**		
		Shrub volume	**0.30 (0.05 – 0.56)**		
	Random effect	Temporal replicate (Intercept) SD = 0.39	0.39 (0.18 – 0.83)		

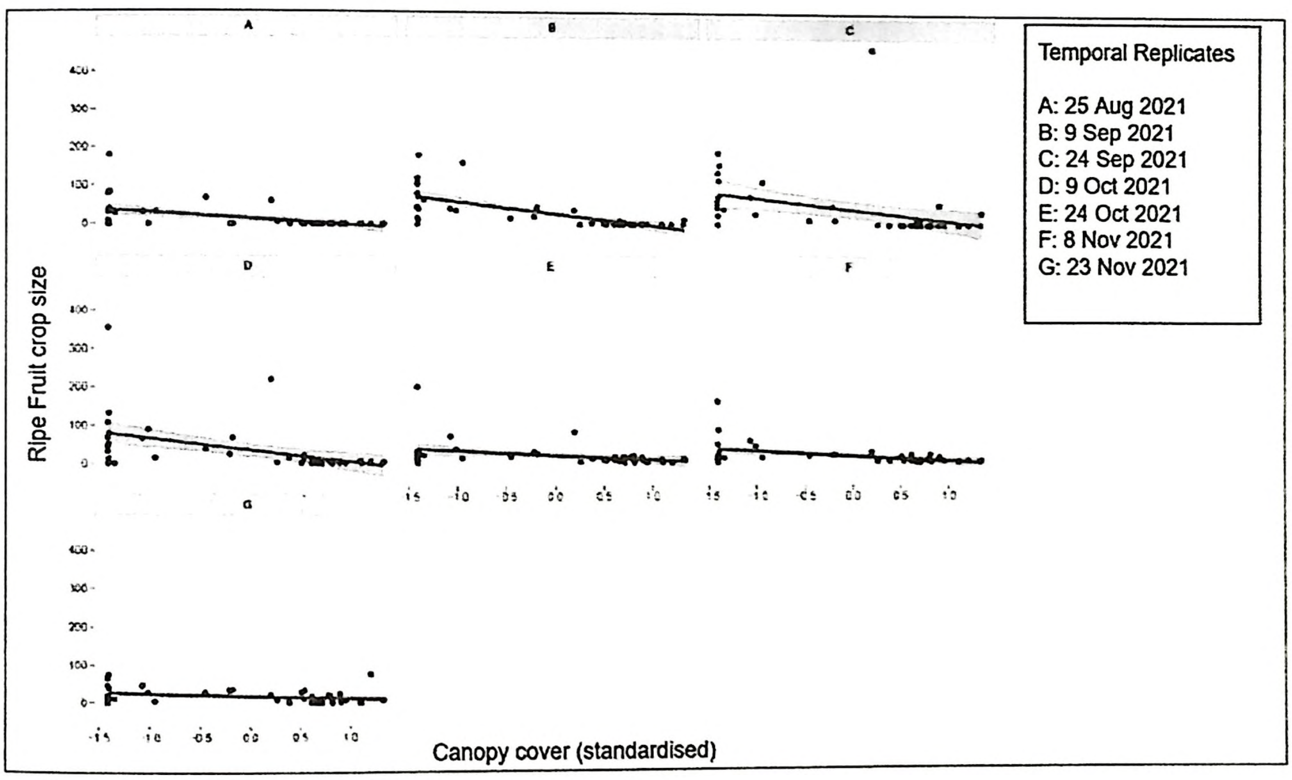

Figure 3. The relationship between ripe fruit crop size and canopy cover for the bushes monitored for phenology. The fruit crop size decreases with increase in canopy cover. The mean (± SD) canopy cover = 37.3% (± 26.4).

Frugivore composition in different habitat types

The results from the 'ANOSIM' analysis showed a significant difference in the composition of frugivores species of *Lantana camara* between open and forest habitats (R = 0.18, p = 0.001, stress = 0.15). However, low R statistic suggests that the dissimilarity between the groups is only marginally higher than the dissimilarity within the groups (Figure. 4).

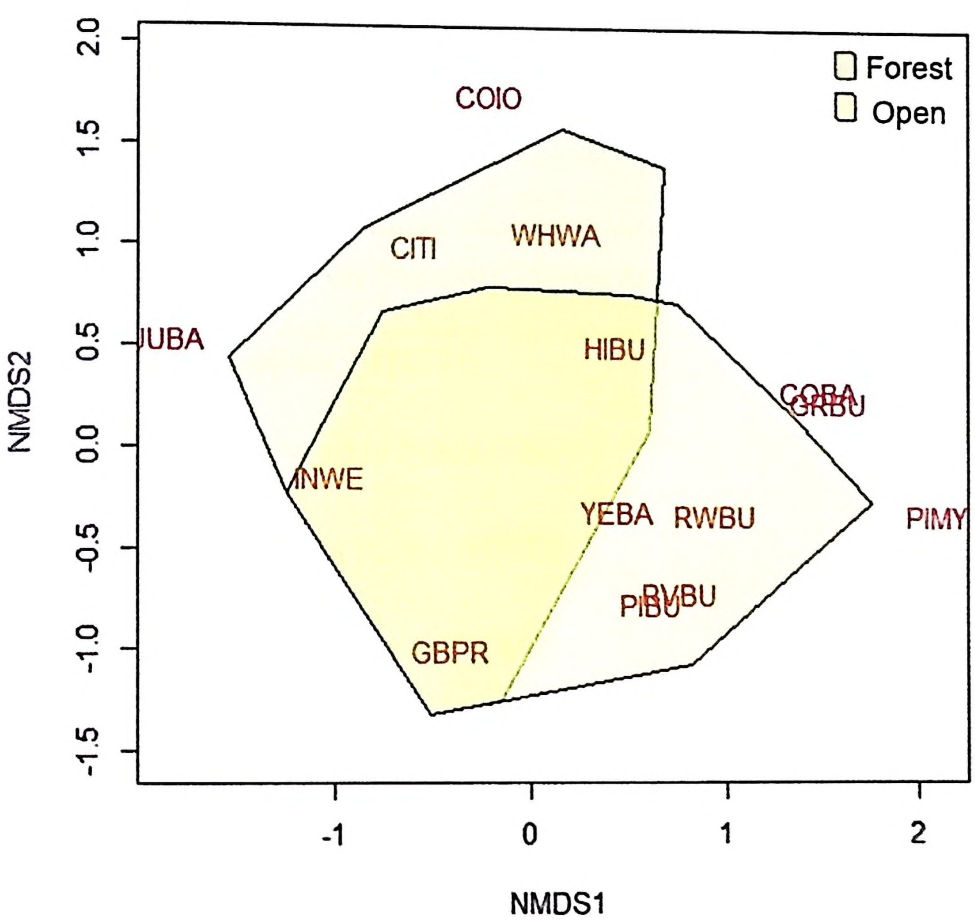

Figure 4. Species composition of frugivores that visited focal *Lantana camara* bushes. The green and yellow polygon covers the sampling units in the forest and open habitat respectively. The red labels shows four-letter species acronym for birds. The bird names along with acronyms has been outlined in the Appendix 2.

Species-level responses to habitat and focal bush characteristics

The MCMC convergence of the HMSC model was satisfactory as the mean potential scale reduction factor (psrf) for the β-parameters (that measure the responses of the species to the environmental covariates) was 1.003 (maximum 1.02). The presence-absence model showed a limited fit to the data, with the mean Tjur's R^2 being 0.14 (maximum 0.32) for the explanatory power. The Tjur's R^2 values for individual species are given in the Table 2.

Table 2. Tjur's R^2 values as obtained from the HMSC presence-absence model for individual frugivore species

Frugivore Species (Species code)	Tjur's R^2
Cinereous Tit (CITI)	0.04
Grey-breasted Prinia (GBPR)	0.1
Himalayan Bulbul (HIBU)	0.14
Indian White-eye (INWE)	0.08
Red-vented Bulbul (RVBU)	0.32
Red-whiskered Bulbul (RWBU)	0.14
Yellow-eyed Babbler (YEBA)	0.13

The results showed that the probability of occurrence on fruiting *Lantana* bush of the three species of Bulbuls was negatively associated with canopy cover (Figure 5). Occurrence of Indian White-eye was positively associated with shrub cover (Figure 5). Yellow-eyed Babbler responded negatively to shrub cover but responded positively to ripe fruit crop size in the neighbourhood of focal bush (Figure 5). Grey-breasted Prinia responded positively to average height of the vegetation cover (Figure 5).

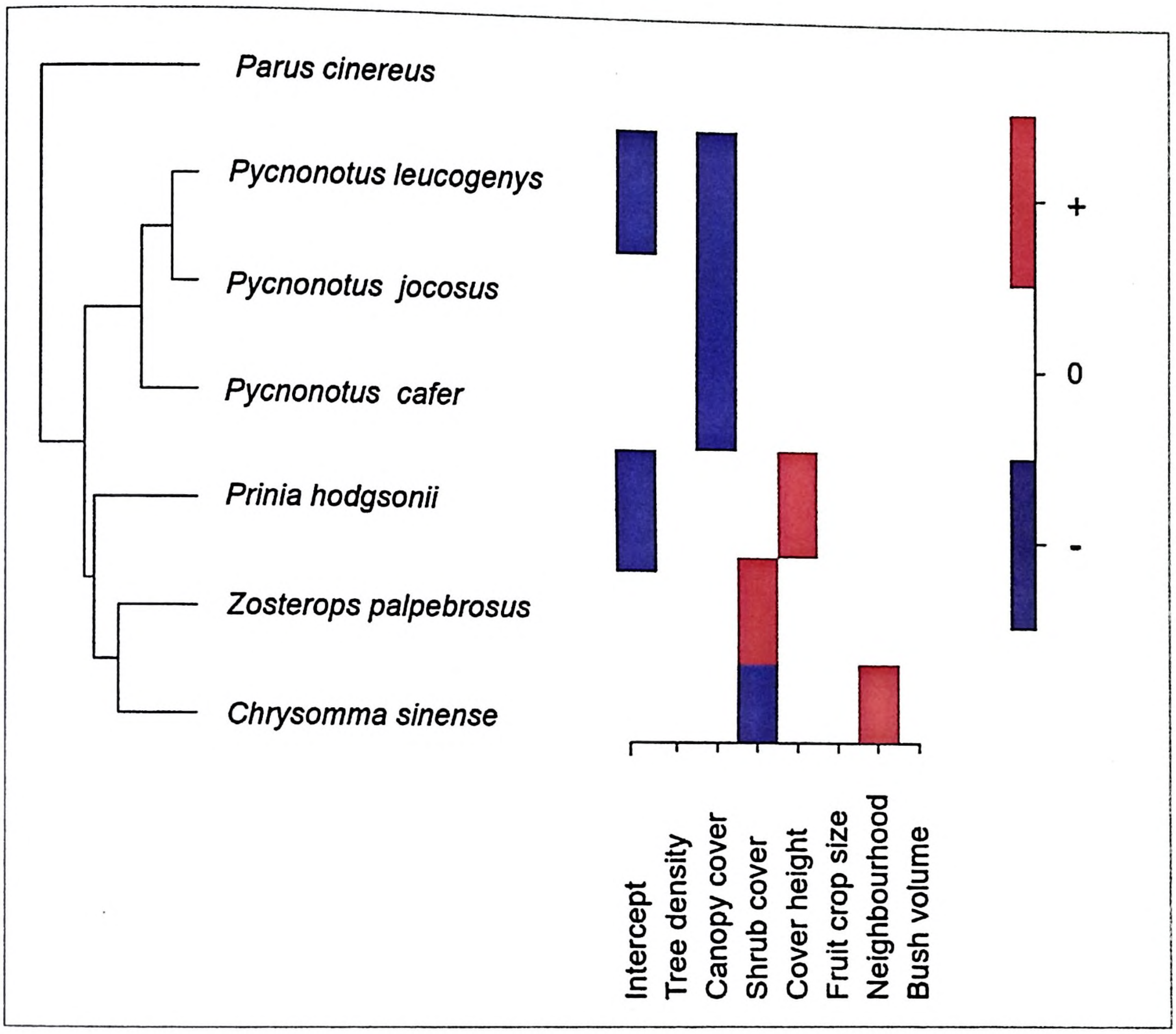

Figure 5. The responses of the species (in rows) to predictor variables (in columns). Positive coefficients with 95% credible intervals not overlapping zero are shown in red, negative coefficients with 95% credible intervals not overlapping zero are shown in blue. The species are ordered according to their phylogenetic relationships as depicted in the phylogenetic tree in the left of the figure.

Variance partitioning suggested that canopy cover explained most variation in the occurrence of the frugivore species followed by tree density and fruit crop size (Figure 6). I did not find any significant phylogenetic signal in species responses to predictor variables as 95% credible interval around Rho value overlapped zero (ρ = 0.55 (95% CI)). I did not find any association between species traits (beak length, beak width and hand-wing Index) and predictor variables.

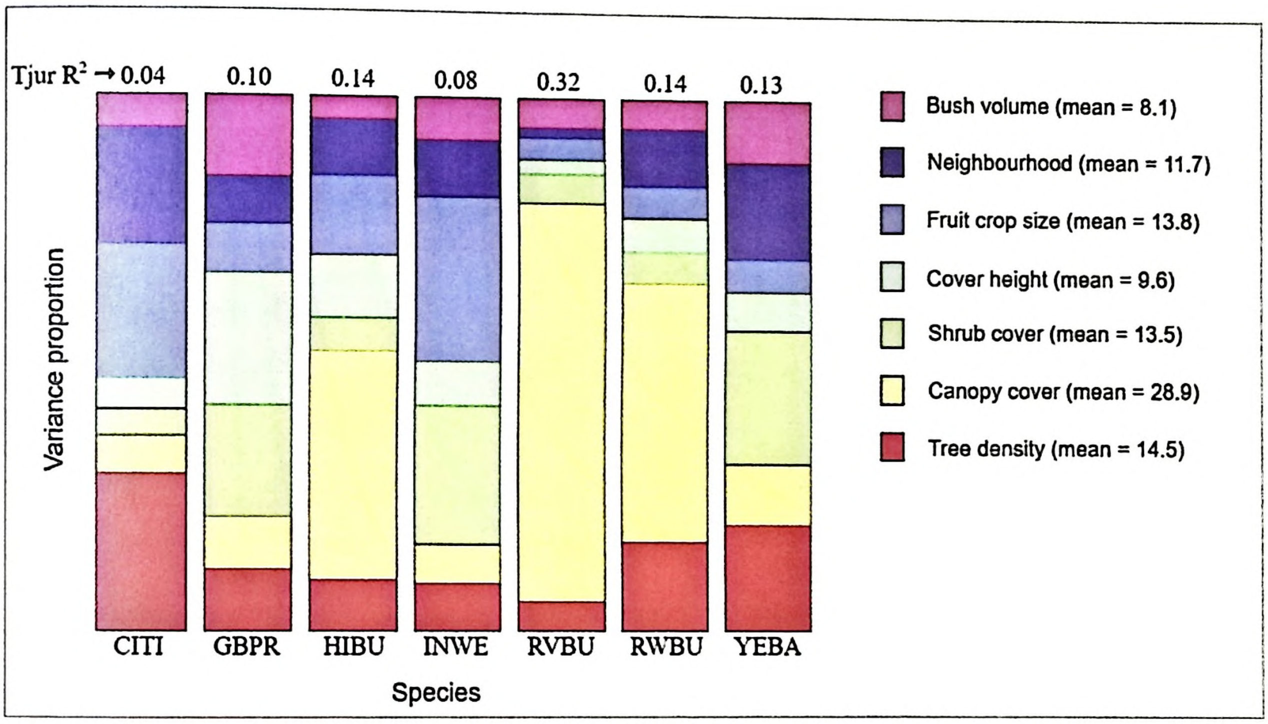

Figure 6. Variance partitioning among explanatory variables included in the model. The legends give the mean (across species) explained variance (in percent) by different predictors. Values above each bar is the Tjur's R^2 value (total explained variation) for the respective frugivore. The species have been ordered alphabetically.

Seed Dispersal Effectiveness (SDE) landscape

The most effective dispersers included Red-vented Bulbul (RVBU), Himalayan Bulbul (HIBU) and Indian White-eye (INWE) (Figure 7). The other seed dispersers included in the analysis were Cinereous Tit (CITI), Jungle Babbler (JUBA), Common Babbler (COBA), Grey Bushchat (GRBU) and Common Iora (COIO). These birds had very low visitation rates and swallowed proportionally less fruit during the focal observations.

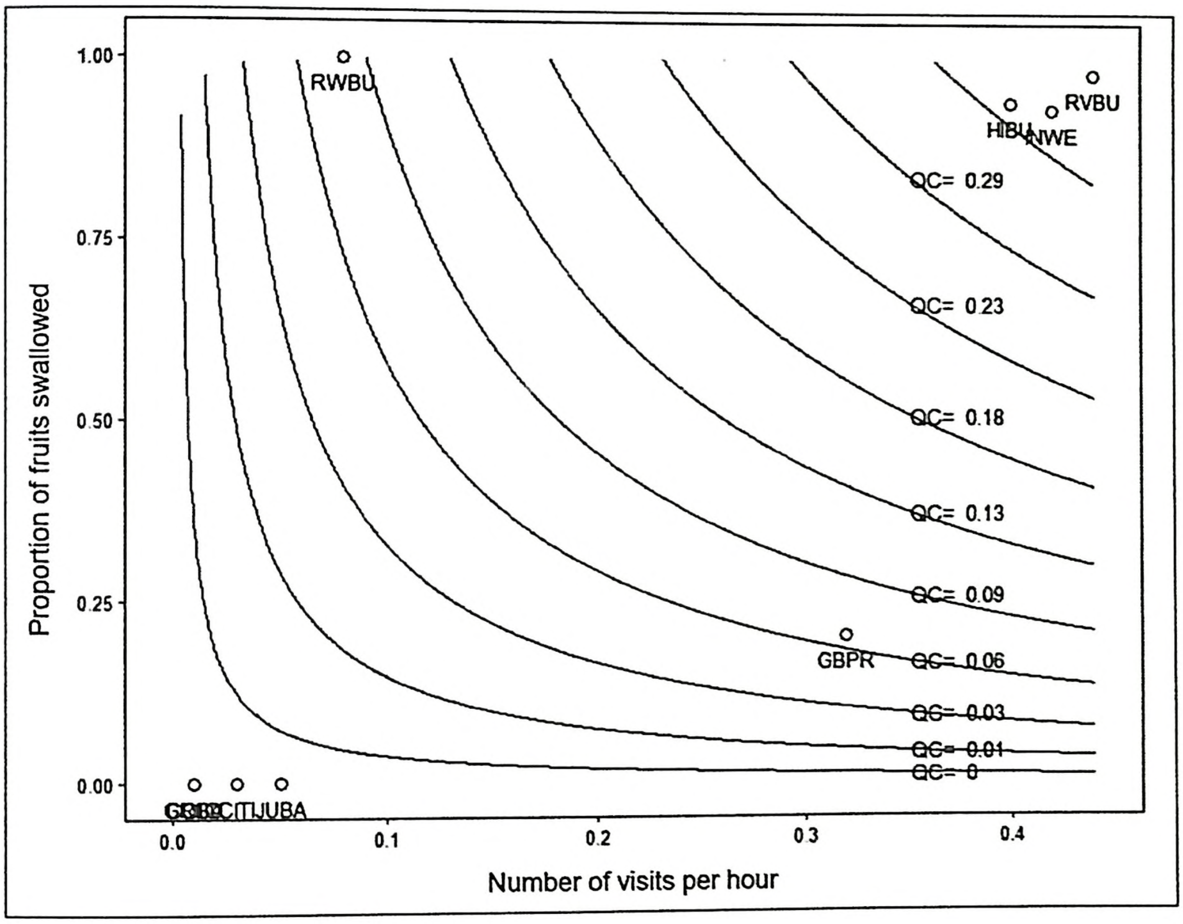

Figure 7. The seed disperser effectiveness (SDE) landscape of the seed dispersers of *Lantana camara.* Each point represents the product of mean visitation rate and the proportion of fruits swallowed by each frugivore species. The isoclines represent all possible combinations of the quantitative and qualitative component that yield the same QC value. The most effective seed dispersers identified were Red-vented Bulbul (RVBU), Himalayan Bulbul (HIBU) and Indian White-eye (INWE).

Drivers of visitation patterns of seed dispersers

The number of visitations of effective seed dispersers were negatively influenced by average Canopy cover above the focal bush (Table 3, Figure 8). I failed to find significant influence of the remaining habitat and focal bush variables on the number of visitations of effective seed dispersers.

Table 3. GLM coefficients (for standardised parameters) and their 95% confidence intervals for the relationship between number of visitations of effective seed dispersers on focal bush per three hours and habitat as well as focal shrub variables. Parameter coefficient(s) with 95% CIs not overlapping zero have been highlighted in bold. The McFadden's pseudo R^2 for the model has been shown.

Response variable	Predictor variable	Estimate (95% CI)	Pseudo R^2
Number of visitations of effective seed dispersers on focal bush per three hours.	**(Intercept)**	**1.19 (0.90 – 1.5)**	**0.13**
	Canopy cover	**-0.43 (-0.80 – -0.04)**	
	Tree density	0.04 (-0.30 – 0.41)	
	Shrub cover	-0.002 (-0.39 – 0.38)	
	Cover height	0.33 (-0.04 – 0.72)	
	Neighbourhood fruit crop size	-0.09 (-0.48 – 0.33)	
	Fruit crop size	0.23 (-0.10 – 0.8)	
	Focal shrub volume	0.03(-0.31 – 0.38)	

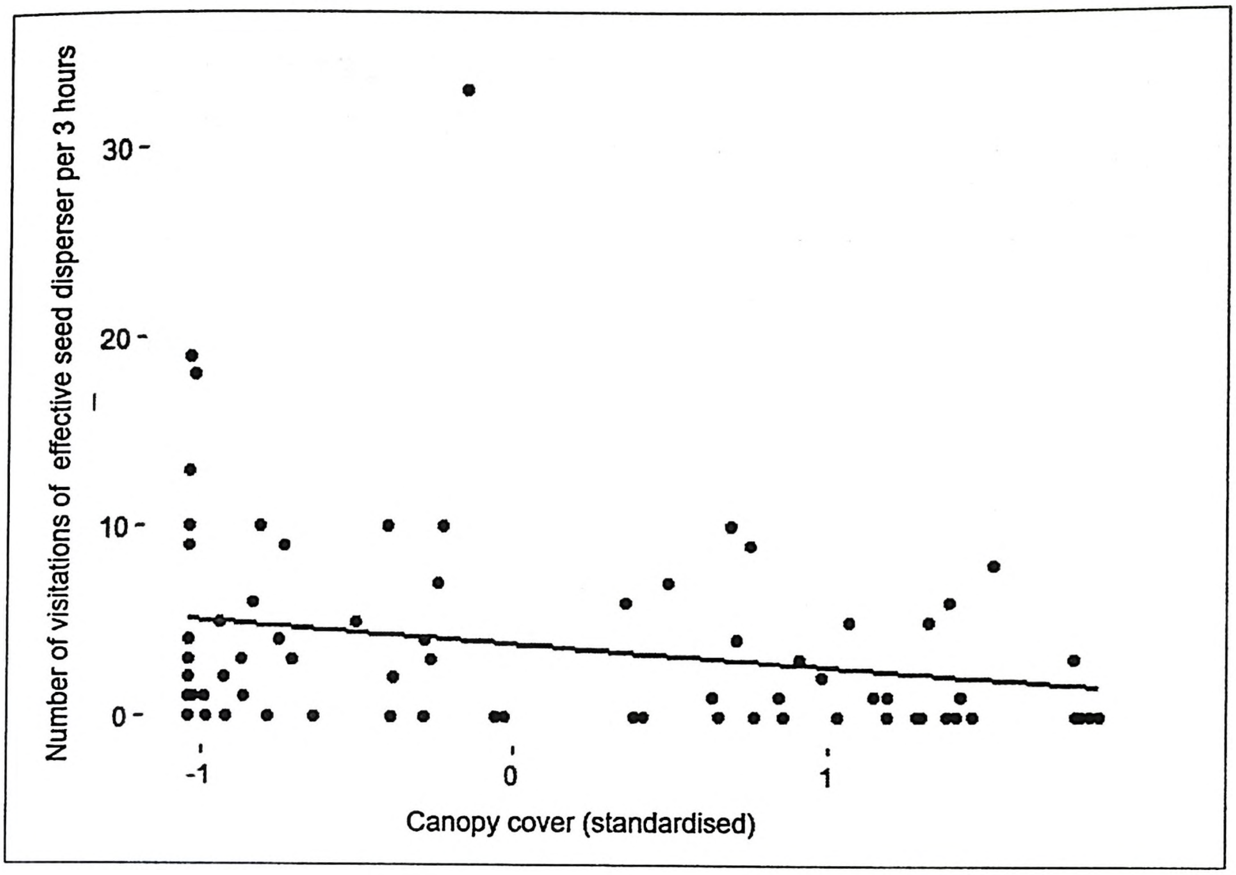

Figure 8. Relationship between number of visits of effective seed dispersers on the focal bush per three hours and standardised values of average canopy cover above the focal bush. The average (± SD) canopy cover over the focal bushes was 23.36% (± 22.48).

DISCUSSION

My results showed that *Lantana* bushes in low canopy cover produced more fruits and got more visitations of effective seed dispersers. Together these results suggest that reproductive output as well as the chances of seed dispersal of *Lantana* was governed by the openness of canopy.

Canopy cover and reproductive output in *Lantana*

One of the major findings of the results were the positive response of fruit crop size of *Lantana* to canopy openness over the bush. Previous studies have found positive influence of canopy openness on the *Lantana* abundance (Fensham et al., 1994; Khaniya and Shrestha, 2020; Paulsamy et al., 2010; Sundaram and Hiremath, 2012; Totland et al., 2005). Similar response of higher abundance has also been demonstrated for other open-habitat alien invasive species (Baret et al., 2008; Gómez et al., 2019). For *Lantana*, the relative growth rates and germination is also shown to be higher at sites with lower canopy cover (Duggin and Gentle, 1998; Raizada et al., 2008). Enhanced growth rates and high germination rates have been postulated as the most likely mechanism for higher abundance and ground cover of open habitat invasive species such as *Lantana* (Charbonneau and Fahrig, 2004). Studies assessing influence of canopy on *Lantana* has largely focused on vegetative success. However, influence of canopy cover on fruit production and seed dispersal has received very sparse attention (but see Totland et al., 2005). One previous study demonstrated that low canopy cover was associated with greater *Lantana* cover but not with fruit crop size

(Totland et al., 2005). Contrary to this, results from this study suggests that, while open canopy may lead to faster vegetative growth in *Lantana,* it also likely results in greater fruit production. For a fleshy-fruited invasive like *Lantana,* higher reproductive output in fruit production has implications for its invasion via seed dispersal. Therefore, this study adds a novel insight into the reproductive response of an invasive to variation in canopy cover.

Canopy cover and seed dispersal of *Lantana*

The higher visitation rates of seed dispersers at sites with lower canopy cover provides further insight. Visitation rates of effective seed dispersers are reliable indicators of fruit removal rate (Schupp et al., 2010). Removal of fruits by effective seed dispersers is most likely to lead to the seed dispersal (Jordano and Schupp, 2000). Thus the higher visitation rates implies, that in addition to the higher reproductive output, the chances of seed dispersal of *Lantana* are also higher in relatively open canopy sites. Together, this suggests the increased chances of spread of the invasive, particularly in open habitats

Role of the Bulbuls in *Lantana* seed dispersal

Bulbuls are among the key seed dispersers of small-seeded plants in wet and dry Asian tropics (Gopal et al., 2020; Naniwadekar et al., 2019; Ramaswami et al., 2017). They have higher visitation rates on fruiting plants, and swallow and disperse seeds of small-seeded plants well (Naniwadekar et al., 2019). In my study too, two of the three most effective seed dispersers of *Lantana,* are Bulbuls, including Red-vented Bulbul and

Himalayan Bulbul. Probability of visitation of all three Bulbul species was negatively associated with canopy cover. This can be explained by higher abundances of Bulbuls, especially the Red-vented and Himalayan Bulbuls in open habitat as compared to closed forests (as inferred by replicated point-count surveys across the habitats) (Taneja et. al. unpublished data, Appendix 3). Since the Bulbuls formed ~67% of the total visitations of effective seed dispersers, it is likely that the higher visitation rates on *Lantana* in relatively open areas could be driven by higher abundance of Bulbuls in open habitats.

Role of White-eyes in *Lantana* seed dispersal

In this study, Indian White-eye are also an effective seed disperser of *Lantana* along with the Bulbuls. Previous studies have also identified other species of White-eyes as key seed dispersers for small-seeded plants including *Lantana* (Corlett, 1998; Kawakami et al., 2009; Pliosungnoen, 2007). Interestingly though, studies have also highlighted the reduced diversity of fruits in the diet of White-eyes as compared to the Bulbuls, owing to their gape limitations (Corlett, 1998). This can potentially mean higher importance of *Lantana* in the diet of White-eye as compared to the Bulbuls. The visitation rates of Indian-white eye on *Lantana* are comparable, as are their abundances for both the habitats

The probability of frugivore visitation on *Lantana* itself was determined by different choices of habitat features. The habitat use decisions of frugivores is a trade-off between habitat preferences, fruit availability and minimizing predation risk (García and Ortiz-Pulido, 2004; Martínez and García, 2015). While Bulbuls visitation on *Lantana* was higher in relatively open-canopy habitats, presence of shrub cover around the focal positively influenced the visitation of White-eyes on *Lantana*. The presence of shrub cover may be important for the small frugivores like White-eyes to minimise predation (García et al., 2011).

The fruit tracking hypothesis predicts that frugivores respond positively to the fruit abundance at multiple spatial scales from fruits on a stem to across patches varying in fruit availability (García and Ortiz-Pulido, 2004). I failed to find evidence of the fruit tracking hypothesis at the scale of the fruiting *Lantana* shrub. Both the occurrence probability of frugivores and the visitation rates of effective seed dispersers on *Lantana* didn't respond significantly to the fruit crop sizes of the focal bush. This implies that the fruit resources may not be tracked at the scale of investigation. Sympatric frugivores are known to track fruit resources at multiple spatial scales (Naniwadekar et al., 2015). Sympatric Bulbuls were found to track fruit resources at different scales in scrub thorn forests in south Indian (Jayanth, 2020). In this case, frugivores, especially Bulbuls, could be present in higher numbers in open forests due to the greater availability of *Lantana* fruits (given the greater fruit crop sizes), particularly in this season when not many other species are fruiting. Apart from greater fruit crops, the cover of *Lantana* is likely higher in open forests, which may make them attractive fruiting hubs (Carlo et al., 2007). Additionally, dilution effects owing to the abundant availability of *Lantana* as a food resource could be one of the other reasons for failing to find evidence for fruit resource tracking since frugivores may feed on any shrub irrespective of its fruit crop size. Optimization for tracking fruits is also likely to be outweighed by the availability of the other limiting factor, i.e. habitat features in this case that would decrease predation risk (García et al., 2011; Martínez and García, 2015). Thus, frugivores may not always track shrubs with the largest fruit crop size but may also require additional features perceived as important by the frugivores. This, too, may influence the relationship between fruit crop size and frugivore visitations on fruiting shrubs.

Conservation implications of the study

Lantana camara is pervasive across multiple habitats in the Shivalik hills. Among the different human activities in these forests include lopping branches of trees. Trees are lopped as fodder for cattle by the local communities (Harihar et al., 2009). Lopping leads to reduction in canopy cover (Malik et al., 2016), thus, resulting in greater fruit production and seed dispersal. Similar impacts can be expected in other regions where selective logging and other human activities that cause an increase in canopy openness.

A recent study demonstrated that active *Lantana* removal is implemented at much smaller spatial scales than the home ranges of their main seed dispersers, the Bulbuls (Ramaswami et al., 2016). Thus, removal of *Lantana* is not likely to be successful since seed dispersers may continue to bring seeds into the nearby areas. This study also suggests that *Lantana* removal should prioritise shrubs in open forests or forest edges since they are likely to fruit much more than shrubs inside closed forests.

Limitations of the study

A potential limitation of this study is that the fruit tree watches were not conducted till the end of the fruiting season of *Lantana*. This could not be carried out due to logistical constraints. However, the study covered the peak fruiting period of *Lantana*. I have continued phenology monitoring of *Lantana*, and the fruit availability is decreasing, and there is unlikely another fruiting peak this season. I watched 80 fruiting shrubs of *Lantana*. This robust sample size gives me confidence in the observed results. Despite including habitat and focal bush variables, the explained variation in visitation rate of effective seed dispersers was limited. This highlights the need to include additional predictor variables (e.g., availability of other food resources in addition to *Lantana*) and examine the relationships at multiple spatial scales in the future.

Overall, our study suggests the role of canopy openness as a critical habitat feature in determining the fruit abundance and visitation rates of seed dispersers on *Lantana*. This study thus highlights the higher susceptibility of relatively open habitats to the invasion of *Lantana* via the mechanism of vertebrate-mediated seed dispersal. Even at patch scales, high propagule pressure is shown to act as source populations to mediate invasion in surrounding intact habitats (Alston and Richardson, 2006). Thus, this study also has implications for the lopped or fragmented forests (edge effects) where greater canopy openness may facilitate the spread of fleshy-fruiting invasive species through seed dispersal.

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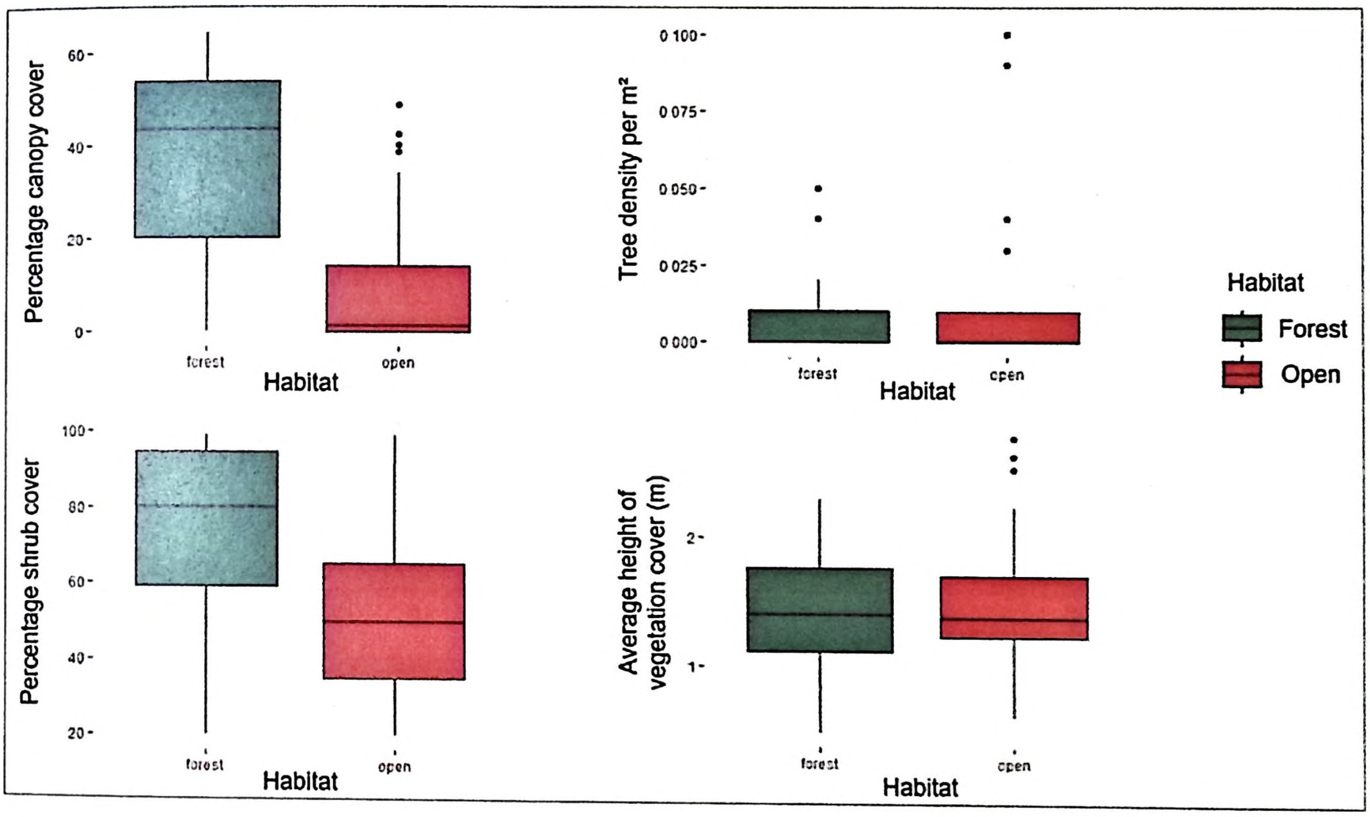
APPENDICES

Appendix 1. Figure showing variation in habitat characteristics between the broad open and the forest habitats. The characteristics including canopy cover, tree density, shrub cover and vegetation height were measured in a 10 m radii plot from the centre of the focal *Lantana* bush.



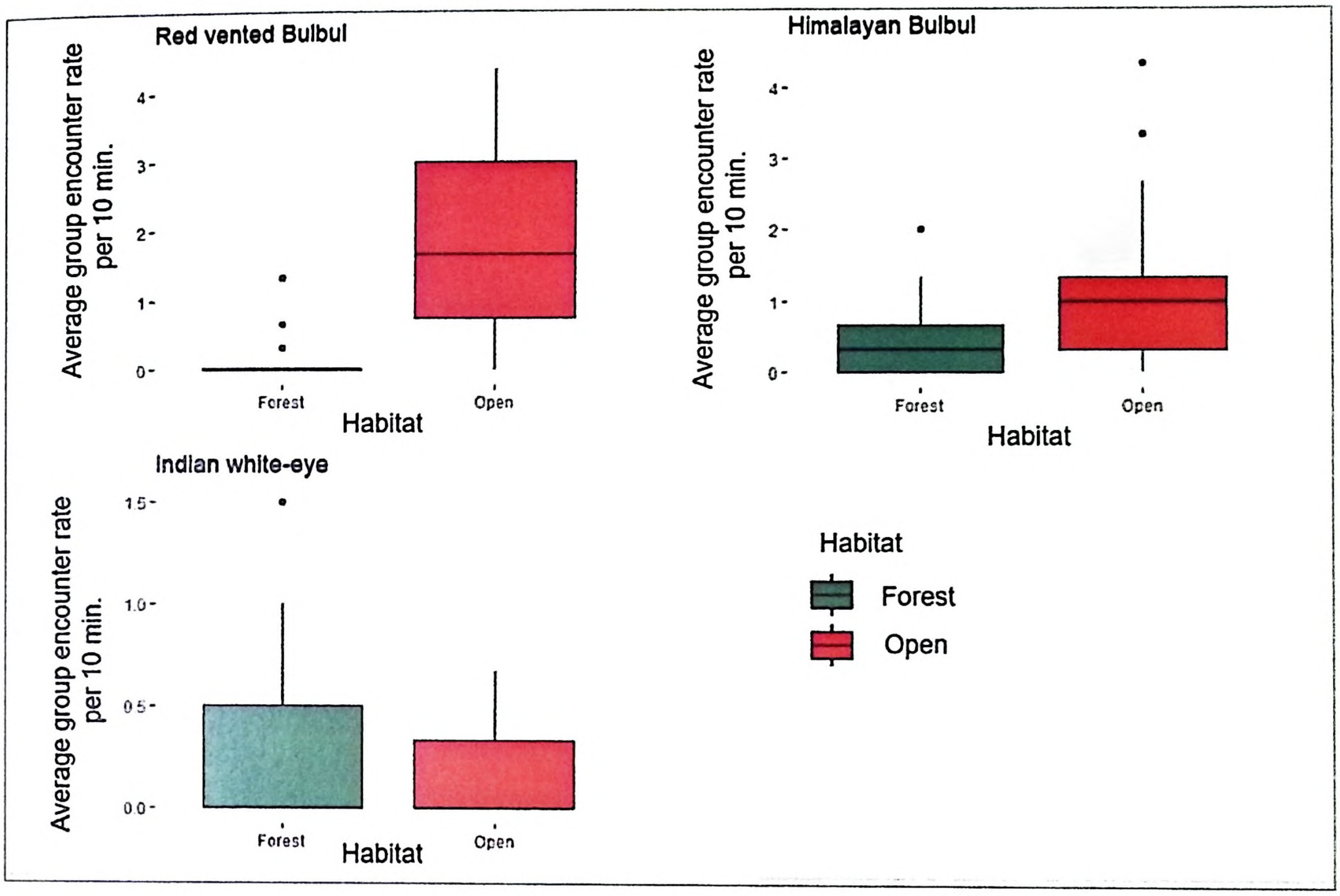
Appendix 2. Summary of visitation and fruit handling behavior of frugivores from the 80 focal *Lantana* watches.

Frugivores of *Lantana* (Species Code)	Total visits in Open habitat (n=40)	Total visits in Forest habitat (n=40)	Duration of focal observation (minutes)	Total number of fruits handled	Total number of fruits swallowed
Asian Pied Starling* (PIMY)	2	0	-	-	-
Cinereous Tit** (CITI)	4	4	1	4	0
Common Babbler* (COBA)	3	0	-	-	-
Common Iora** (COIO)	0	2	2	0	0
Grey-breasted Prinia (GBPR)	36	40	6	5	1
Grey Bushchat (GRBU)	3	0	2	0	0
Himalayan Bulbul (HIBU)	76	21	27	52	49
Indian White-eye (INWE)	53	48	49	43	40
Jungle Babbler** (JUBA)	0	12	10	0	0
Pied Bushchat (PIBU)	1	1	-	-	-
Red-vented Bulbul (RVBU)	103	2	32	66	65
Red-whiskered Bulbul (RWBU)	18	0	1	4	4
Whistler's Warbler (WHWA)	2	1	1	0	0
Yellow-eyed Babbler* (YEBA)	19	0	-	-	-

* COBA, PIMY and YEBA were opportunistically observed feeding on fruits on bushes other than the focal bush.

** CITI, JUBA and COIO were considered as Seed dispersers based on data from Ramaswami et al., 2016

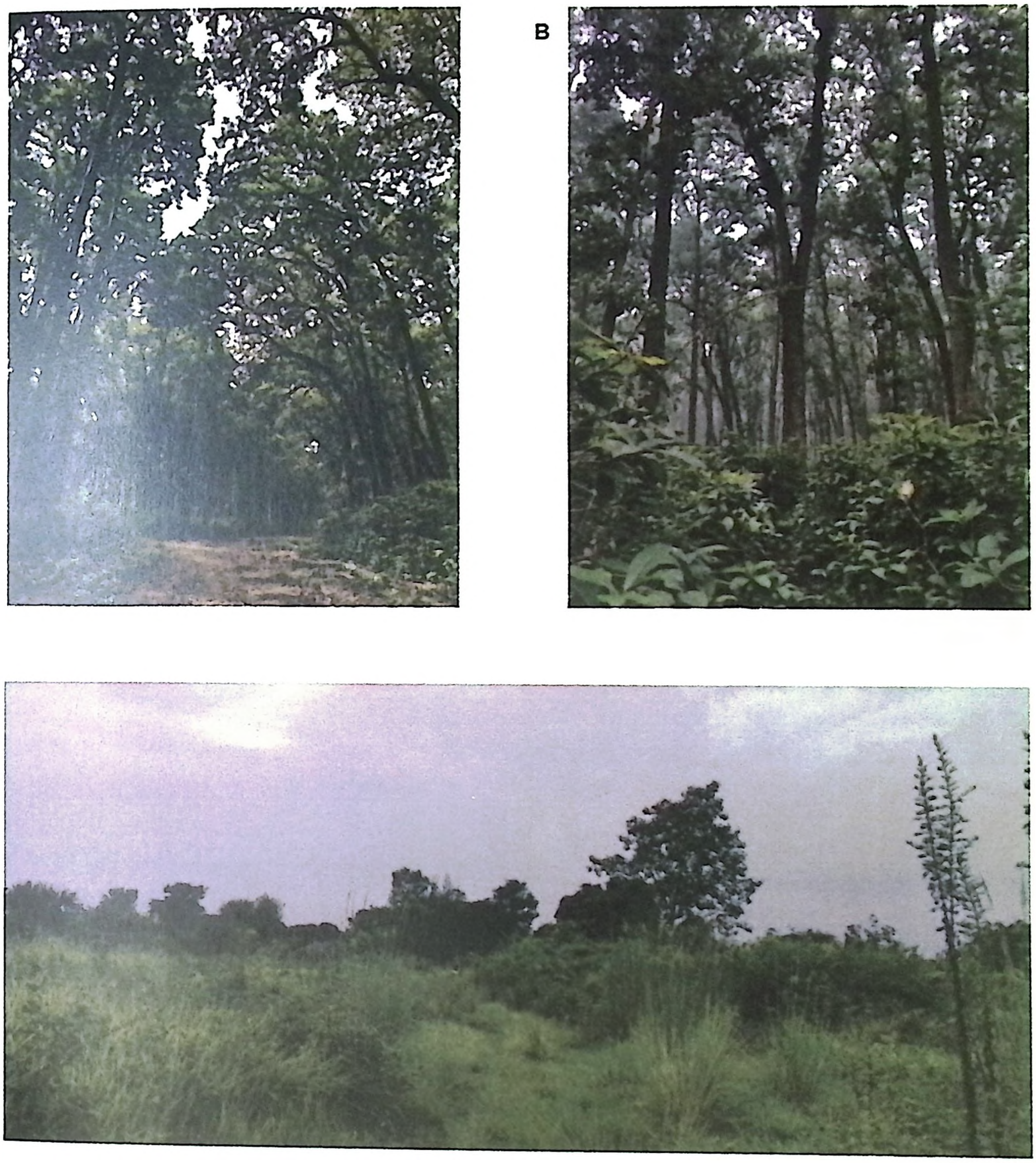
Appendix 3. Figure showing average group encounter rates of effective seed dispersers of *Lantana*. This was calculated by averaging the number of group encounters of the species from three replicates of point count surveys at each focal bush.



Appendix 4. Images of habitats showing variation in canopy cover. Panel A and B shows the forest edge (fire-line) and forest interior respectively. Panel C shows the open habitat of grassland-shrubland mosaics.

A B

C



Appendix 5. Monitoring fruiting phenology of marked *Lantana* bushes. Ripe fruit crop size was recorded for all 45 focal phenology bushes fortnightly during the study period.

Appendix 6. Mean and Median distances among the Sampling units (Focal *Lantana* bushes) in each sampling site.

Site	**Habitat**	**Mean distance (m)**	**Median distances (m)**
Sal forest Asarori	Forest	348.1	331.5
WII grassland-shrubland	Open	132.77	86.63
Residential grassland-shrubland	Open	69.41	66.77
Chandrabani grassland-shrubland	Open	124.31	112.02

Appendix 7. Grazing of cattle and lopping of *Terminalia elliptica* for fodder were the major disturbances observed in the forest.