

# JOURNAL OF AVIAN BIOLOGY

## Article

### Gardeners of the forest: hornbills govern the spatial distribution of large seeds

Rohit Naniwadekar, Charudutt Mishra, Kavita Isvaran and Aparajita Datta

R. Naniwadekar (<https://orcid.org/0000-0002-9188-6083>) ✉ ([rohit@ncf-india.org](mailto:rohit@ncf-india.org)), C. Mishra and A. Datta, Nature Conservation Foundation, Mysuru, Karnataka, India. RN also at: Manipal Univ., Manipal, Karnataka, India. CM also at: Snow Leopard Trust, Seattle, WA, USA. – K. Isvaran, Centre for Ecological Sciences, Indian Inst. of Science, Bengaluru, Karnataka, India.

#### Journal of Avian Biology

2021: e02748

doi: 10.1111/jav.02748

Subject Editor: Tomas Carlo  
Editor-in-Chief: Jan-Åke Nilsson  
Accepted 16 August 2021



Seed dispersal by frugivores is vital to the maintenance of tree diversity in tropical forests. However, determining the influence of different frugivores over the distribution of their food plants is difficult, given the complexity of these interactions in the tropics. Consequently, most studies have been restricted to small scales, examining seed dispersal and establishment associated with nests, roosts or fruiting trees. Here, we evaluate the role of frugivorous hornbills in dispersing seeds at spatial scales of 1 ha. We monitored hornbills and seed rain at a tropical forest site in north-east India. We quantified the abundance of hornbill food plants and recruits of large-seeded plants. We estimated removal rates of dispersed, large seeds to determine post-dispersal seed fate. We found that the distribution of large-seeded canopy food plants influenced the distribution of the relatively abundant *Rhyticeros undulatus*. The overall distribution of hornbills resulted in spatially contagious seed rain patterns for the large-seeded plant species. Patches with canopy food plants had a higher recruit diversity. Our results show positive feedback between distribution of rare but important hornbill food plants, hornbills and distribution of seeds and saplings of large-seeded plants in the landscape. Widespread loss of hornbills due to hunting and habitat loss in the region have likely disrupted these feedback mechanisms that are critical for tree species regeneration.

Keywords: Asian tropical forests, large-bodied frugivores, Namdapha, rare-biased seed dispersal, rufous-necked hornbill *Aceros nipalensis*, spatially contagious seed dispersal, wreathed hornbill *Rhyticeros undulatus*

#### Introduction

Animal-mediated seed dispersal is a crucial step in the life history of up to 90% of tropical plants as it provides the initial template for plant regeneration (Jordano 2000). Among vertebrates, birds are key seed dispersers. In tropical forests, birds can disperse seeds of up to 75% of tree species and 60% of shrub species (Wenny et al. 2016). The patterns of dispersal of seeds by a frugivore are not random. Seeds tend to get disproportionately dispersed at sites preferred by the frugivore (Wenny and Levey 1998, Russo and Augspurger 2004, Kitamura et al. 2008, Viswanathan et al. 2015), leading



[www.avianbiology.org](http://www.avianbiology.org)

© 2021 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

to spatially contagious seed dispersal (Schupp et al. 2002, Kwit et al. 2004). Spatially contagious seed dispersal implies that frugivores non-randomly disperse seeds over space, with some sites having higher seed arrival rates than others. For example, seeds are often clump dispersed under nest or roost sites of seed dispersers with favourable or unfavourable outcomes for plant regeneration (Kinnaird 1998, Russo and Augspurger 2004, Kitamura et al. 2008).

Frugivores track resources, often at multiple spatial scales (García and Ortiz-Pulido 2004, Naniwadekar et al. 2015c). For example, frugivores may track individual trees with large fruit crop sizes (small scale) or patches with a higher abundance of fruiting trees (large scale) (García and Ortiz-Pulido 2004, Naniwadekar et al. 2015c). Therefore, spatially contagious seed dispersal can potentially occur at multiple scales. However, our understanding of spatially contagious seed dispersal at large spatial scales is relatively poor. Spatially contagious seed dispersal at large scales can have implications for the organization of fleshy-fruited plant communities, in turn influencing distributions of frugivores. The spatially contagious distribution of frugivores and their food plants will likely result in positive feedback, as has been suggested by Lázaro et al. (2005). However, past studies have focused on small spatial scales. They have examined spatially contagious seed dispersal at roost sites (Russo and Augspurger 2004, Kitamura et al. 2008) or con- and hetero-specific fruiting trees (Clark et al. 2004, Kwit et al. 2004, Viswanathan et al. 2015, Trolliet et al. 2017) or in the immediate neighbourhood of fruiting trees (Chanthorn et al. 2018). This highlights the need to understand patterns and underlying processes governing spatially contagious seed dispersal at large spatial scales and its implications for maintaining plant diversity in the tropics. However, it is challenging to determine the role of frugivores in the spatial distribution of seeds, given the diverse array of fleshy-fruited plants and their seed dispersers.

Asian hornbills are large-bodied frugivores that feed on a diverse array of fruit species (of varying seed sizes) and track these fruit resources at multiple spatial scales (Kinnaird et al. 1996, Kinnaird and O'Brien 2007, Naniwadekar et al. 2015c). Hornbills are responsible for long-distance seed dispersal (Naniwadekar et al. 2019b). They are particularly crucial for several large-seeded plants as they disperse higher numbers of seeds than other frugivores (Naniwadekar et al. 2019a, 2021a). Unlike the small-seeded plants, these large-seeded plants have a relatively small assemblage of frugivores that can effectively disperse their seeds, with hornbills being the most important (Naniwadekar et al. 2019a, 2021a). Therefore, hornbills and large-seeded hornbill food plants provide an opportunity to examine potential positive feedback mechanisms, in which the food plants govern the distribution of hornbills, who disperse the seeds in a spatially contagious manner and thereby influence the distribution of the food plants. Given that only a small proportion of seeds are likely clump-dispersed by hornbills at nests (females incarcerated inside nest cavities) and roost sites (Naniwadekar et al. 2019b, 2020), hornbills can be expected to scatter-disperse seeds in low densities during their daily foraging, especially

in the non-breeding season. Seeds that are scatter dispersed should have greater chances of recruitment due to a lower influence of negative density-dependent factors like seed predation (Howe 1989).

We studied hornbills and their important large-seeded food plant species to understand better the role of frugivores in governing the spatial distribution of seeds with potential implications for plant recruitment. Given that hornbills often track resources at large scales, we hypothesized that patches (1 ha) with a high abundance of hornbill food plants attract hornbills and serve as seed dispersal foci, facilitating spatially contagious seed deposition and recruitment of fruiting plants consumed by hornbills. First, we examined whether hornbill encounter rates were positively associated with the abundance or presence of different fruit resources. Next, we examined whether the scatter-dispersed seed rain of large-seeded species was positively associated with hornbill encounter rates. Finally, we determined whether the diversity of recruits of large-seeded species was positively influenced by the distribution or abundance of particular fruit plants.

## Material and methods

### Study area

We carried out the study during the non-breeding season of the hornbills (the breeding season is from April to August) over two years from November 2010 to March 2011 (Year 1) and December 2011 to February 2012 (Year 2) on the Hornbill Plateau in the Namdapha Tiger Reserve in India (Supporting information; area: 1985 km<sup>2</sup>; elevation range: 200–4570 m a.s.l.). Namdapha is in the easternmost part of the Eastern Himalaya Biodiversity Hotspot (Myers et al. 2000). The Hornbill Plateau (elevation range: 550–800 m a.s.l.), in the western portion of the Reserve, is spread over an area of approximately 15 km<sup>2</sup> (Supporting information). *Terminalia myriocarpa*, *Altingia excelsa*, *Shorea assamica*, *Schima wallichii*, *Beilschmiedia assamica*, *Saprosma ternatum* and *Baccaurea ramiflora* are some of the dominant trees on the plateau. Five species of hornbills occur on the plateau: *Buceros bicornis* (2155–4000 g), *Aceros nipalensis* (2270–2500 g), *Rhyticeros undulatus* (1360–3560 g), *Anorrhinus austeni* (710–900 g) and the *Anthraceroceros albirostris* (600–1050 g) (Naniwadekar and Datta 2013, Poonswad et al. 2013). The densities of hornbills in Namdapha are among the highest reported in Asia (Naniwadekar and Datta 2013). We focused on the three larger hornbill species, *B. bicornis*, *A. nipalensis* and *R. undulatus*.

### Frugivore visitations on fruiting trees

We wanted to independently validate that hornbills were the primary consumers of select large-seeded plants. Therefore, we focused on five important fruiting plant species for hornbills that have large seeds (seed width > 15 mm following Naniwadekar et al. 2019a) and which occur in varying

densities in the field site (Table 1; Supporting information). The two species *Canarium strictum* and *B. assamica* can comprise more than 50% of the diet of *R. undulatus* (Naniwadekar et al. 2015c). These two species, along with *Dysoxylum*, can comprise more than 22% of the diet of the *A. nipalensis*. *B. bicornis*, whose diet consists mostly of figs, also consumes these species (Datta and Rawat 2003, Naniwadekar et al. 2015c). To determine the relative importance of hornbills vis-à-vis other frugivores in the seed removal of such species, we carried out focal tree observations (Table 1). A single observer sat under or just beyond (up to 15 m) the tree canopy, camouflaged in the undergrowth but with a clear view of a large proportion of the canopy, and observed focal trees between 05:30 and 11:00 h. For one tree, the watch extended up to 15:25 h. On average, the length of the tree watch was about 4 h 15 min (total effort: 108 h 5 min) (Table 1). We recorded the frugivore species identity and the number of individuals visiting the focal tree. Hornbills and imperial pigeons (*Ducula* spp.) are known to swallow and regurgitate large seeds unharmed.

On the other hand, smaller avian frugivores peck and drop a large proportion of large-seeded fruits during foraging (Naniwadekar et al. 2019a). We classified the different visitors/frugivores into four groups – hornbills, pigeons (large-bodied avian frugivores; 40–50 cm), small-bodied (25–35 cm) avian frugivores (hill mynas, barbets and cochoas) and mammals (primates and diurnal squirrels). We only detected primates/diurnal squirrels in seven out of the 25 focal trees, and they were not observed dispersing seeds of the focal species in these seven sightings. Therefore, we grouped the different mammal species together. When there was a clear view of the frugivore during tree watches, the observer performed focal scans to determine the number of fruits swallowed, dropped and pecked by the focal individual.

### Relationship between hornbill encounter rate and their food plant density

Eight trails, each 1.5 km long and separated by at least 500 m, were marked on the Hornbill Plateau and monitored between 35 and 41 times over the two sampling periods (Supporting information). Using variable-width transect surveys, we recorded information on perched hornbill encounters through repeated trail walks along the eight established trails. One or two observers walked trails in the mornings (05:30–10:30 h) and/or afternoons (12:30–16:00 h). On detecting hornbills during the trail walk, we recorded the species identity and the number of individuals. The total

effort in the first year was 232.5 km and 144 km in the second year. Sampling effort across trails varied between 24.5 and 34.5 km across trails in year 1, but it was the same (18 km per trail) in year 2. We split all the trails into 500 m segments and considered each of the 24 segments (8 trails  $\times$  3 segments of 500 m length each) as a sampling unit (Supporting information). The estimated median seed dispersal distances of hornbills in the non-breeding season is around 250 m (Naniwadekar et al. 2019b), and the length of the segment was twice that distance. Since the habitat was relatively homogenous, we did not expect detection probability to change. Therefore, we used data on hornbill encounter rates (total number of hornbills seen per sampling unit). We only sampled when it was not raining. Previous studies have indicated that hornbill activity patterns do not differ between mornings and late afternoons (Naniwadekar and Datta 2013, Naniwadekar et al. 2019b). Therefore, weather and sampling period were unlikely to affect our results. Additional details of trail walks are in Naniwadekar and Datta (2013).

In each sampling unit, we enumerated hornbill food trees (girth at breast height (GBH)  $\geq$  30 cm) (Supporting information for list of hornbill food plants) within 10 m on each side of the trail (Supporting information). We had prior observations on hornbill food trees from the area (Naniwadekar et al. 2015c). This included enumerating individuals of only those plant species that fruit during the study period irrespective of their fruiting status. Sympatric hornbill species consume varying proportions of figs and other fruits in their diet (Datta and Rawat 2003, Naniwadekar et al. 2015c). We classified the hornbill food plants into 1) figs, 2) canopy food plants and 3) middle-storey food plants. Figs have tiny seeds and fruit crop sizes that are usually a few orders of magnitude larger than the large-seeded hornbill food plants. Canopy food plant species attain large sizes (up to 45 m in height), are large-seeded ( $>1.5$  cm width), and can produce fruit crop sizes that can be several thousand fruits. Middle-storey food plant species grow up to 30 m in height, have small or large seeds, but with fruit crop sizes mostly in hundreds and fewer than 1500 fruits (Supporting information) (Naniwadekar et al. 2015c).

### Relationship between seed arrival and hornbill encounter rate

We cleared the leaf litter on the forest floor and marked 200 plots (1  $\times$  1 m;  $n=1600$  plots across eight trails) using small pegs on either side of each trail. We recorded the species identity and the number of seeds of the large-seeded *C. strictum*, *Phoebe* sp., *Alseodaphne petiolaris*, *B. assamica* and *Dysoxylum*

Table 1. Fruit and seed characteristics of large-seeded tree species observed for determining visitation patterns of frugivores.

Tree species (number of trees observed)	Fruit type	Mean ( $\pm$ SE) seed length (mm)	Mean ( $\pm$ SE) seed width (mm)	Effort
<i>Beilschmiedia assamica</i> (n=7 trees)	Single-seeded drupe	34.3 ( $\pm$ 2.8)	22.9 ( $\pm$ 1.2)	34 h 43 min
<i>Phoebe</i> sp. (n=6 trees)	Single-seeded drupe	27.8 ( $\pm$ 3.6)	16.9 ( $\pm$ 1.0)	24 h 45 min
<i>Canarium strictum</i> (n=4 trees)	Single-seeded drupe	33.8 ( $\pm$ 1.0)	15.1 ( $\pm$ 1.1)	15 h 46 min
<i>Dysoxylum</i> sp. (n=3 trees)	Multi-seeded arillate capsule	28.3 ( $\pm$ 1.0)	17.2 ( $\pm$ 0.5)	12 h 44 min
<i>Alseodaphne petiolaris</i> (n=5 trees)	Single-seeded drupe	35.6 $\pm$ 2.2	17.4 $\pm$ 1.0	20 h 7 min

sp. periodically (Supporting information). The plots were evenly distributed on either side of the trail throughout its length. We considered seeds with no trace of pulp as dispersed seeds. These plots were first established in December 2010 and monitored on seven occasions between January and March 2011 and on six occasions from December 2011 to February 2012. We monitored the plots at intervals of 8–17 days, except once when we monitored them after 28–32 days. The total plot monitoring duration ranged between 69–75 days in the first year and 83–84 d in the second year. We cleared all seeds from the plots after recording the number of seeds. Sixteen of the 24 sampling units had 70 seed monitoring plots, while eight sampling units had 60 plots.

### Seed removal

We wanted to examine whether seeds that are scatter dispersed by hornbills experience high post-dispersal seed removal. We set up plots to estimate the seed removal rate of scatter-dispersed seeds to determine the efficacy of scatter dispersal of seeds. We placed five viable seeds (checked by the water flotation method – seeds that sank in a bucket of water were considered viable), of *C. strictum*, *Phoebe* sp. and *A. petiolaris*, at every 150 m along the eight trails (5 seeds  $\times$  10 points on each trail = 50 seeds per species on each trail), which emulated scatter dispersal (i.e. seeds dispersed at low densities) (Supporting information). We kept seeds of different species in separate plots. These plots were separated from each other by at least 10 m. We marked the seeds using markers with alcohol-based ink, without xylene and toluene to ensure no scent after the ink dried. The marked seeds were not placed under a fruiting tree. We monitored the remaining number of seeds in the plot for 57–85 days. We estimated the number of seeds removed per 100 days for the three species across the 24 sampling units. The number of seed removal plots varied among the 24 sampling units, with eight sampling units having four seed removal plots and 16 sampling units having three seed removal plots (Supporting information).

### Seedling and sapling diversity

In Year 2, we recorded seedlings and saplings of four of the five focal species (*B. assamica*, *Phoebe* sp., *C. strictum* and *Dysoxylum* sp.) in belt transects (1.5 m on each side of trail) along the entire length of the trails. We could not lay plots for two of the 24 sampling units due to logistic constraints. The area covered to record recruits was 500  $\times$  3 m for each of the 22 sampling units. We classified the recruits into two size classes (seedlings: 10–30 cm and saplings: 31–150 cm). We did not record saplings of *Alseodaphne* as we were not able to identify its seedling and sapling.

### Statistical analysis

To determine if hornbills were the key and reliable seed dispersers of the large-seeded plant species, we estimated the visitation rates of different frugivore groups and the proportion

of seeds swallowed by hornbills and small avian frugivores. We compared the effectiveness of different frugivores using the seed dispersal effectiveness landscape and the associated effectiveness isoclines (Jordano 2014). We plotted the visitation rate per hour on the x-axis and the proportion of fruits swallowed on the y-axis.

We first estimated Moran's I to examine spatial autocorrelation in the response variable (total number of hornbills sighted in each sampling unit) using the R package 'ape' (Paradis and Schliep 2018). We used the mid-points of each of the 24 (500 m) segments to determine spatial autocorrelation. We carried out a separate analysis for each hornbill species for each of the two sampling periods. We used generalized linear models (GLM) and zero-inflated models (for *R. undulatus* in Year 2) to explore the relationship between encounters of the three hornbill species (response variable: total number of birds of a hornbill species seen in each sampling unit) and the densities of the two different types of hornbill food plants (continuous predictor: figs and middle-storey food plants) and presence/absence of canopy food plants (categorical predictor). Canopy food plants were rare in the landscape and were detected in four of the 24 sampling units despite exhaustive sampling (24 ha). Therefore, we treated canopy food plants as a categorical (presence/absence) variable. Since GLM with Poisson errors indicated over-dispersion in data, we used the negative-binomial error structure using the R package 'MASS' (Venables and Ripley 2002). For *R. undulatus*, in 2011–2012, we detected 100 birds in only five of the 24 sampling units. Therefore, we used zero-inflated models with Poisson error structure using the R package 'pscl' (Zeileis et al. 2008, Jackman 2020). We used the 'offset' function to control for variable sampling effort.

To investigate the relationship between seed arrival and hornbill encounter rates, we again used GLM with a negative-binomial error structure. We estimated the mean large-seed arrival rate ( $\text{ha}^{-1} \text{day}^{-1}$ ) for each segment for each year. For the GLM analysis that requires count data, we rounded off the large-seed arrival rate. We estimated the mean hornbill encounter rate ( $\text{km}^{-1}$ ) for each segment. Then, we used the overall hornbill encounter rate (all three species combined) as a predictor since any of the three hornbills species could disperse the seeds of the different large-seeded species. In cases where we detected spatial autocorrelation in the response variable (raw data), we examined if the spatial autocorrelation persisted in model residuals following Zuur et al. (2009). The absence of spatial autocorrelation in residuals indicates spatial autocorrelation in seed arrival being explained by the predictor (Zuur et al. 2009).

We estimated the seed removal rates (per 100 days) for three of the five focal large-seeded species. Given the variation in the abundance of seedlings and saplings across the different species, we estimated the Shannon–Weiner diversity index for seedlings and saplings for each of the 22 sampling units. We used the Shannon–Weiner diversity measure as it provides additional information of relative abundance (evenness) apart from species richness. We compared the diversity of seedlings and saplings between plots with canopy food



plants and without canopy food plants, and across the gradient of the abundance of fig trees and middle-storey food plants, to determine the role of each of the different tree types in contributing to the seedling and sapling diversity.

## Results

### Frugivore visitation

During the fruit tree watches, we recorded 15 species, including four hornbill species, two species of pigeons, five species of small avian frugivores and four mammal species (Supporting information). The mean visitation rate ( $\pm$  SE) of hornbills on the different large-seeded plants was 2.3 ( $\pm$  1.2) birds per hour; small frugivores 0.4 ( $\pm$  0.2) birds per hour; mammals 0.1 ( $\pm$  0.04) animals per hour; and pigeons 0.02 ( $\pm$  0.01) birds per hour (Fig. 1). We recorded hornbills swallowing fruits 68% ( $n=47$  fruits) of the time they handled them, while small avian frugivores swallowed fruits only 2% of the time they handled a fruit ( $n=43$  fruits) (Fig. 1). Hornbills were recorded pecking on fruits or dropping them 15% and 17% of the time, respectively. In comparison, the small frugivores were recorded pecking on fruits or dropping them 61% and 35% of the time, respectively (2% of the times we saw them carrying the fruits in their beaks but did not observe whether they dropped or swallowed the fruits). We had no focal feeding observations of two pigeon species (that were detected on only one occasion each during the fruit tree watch) and mammals. We detected primates (hoolock gibbons *Hoolock hoolock* and Assamese macaque *Macaca assamensis*) on three occasions, but they did not feed on the fruits of these large-seeded plants (Supporting information).

### Relationship between hornbill encounter rate and their food plant density

We had 612 and 203 observations of perched hornbills during Year 1 (total effort = 232.5 km) and Year 2 (total effort = 144 km), respectively. The number of individuals of *B. bicornis* (Year 1: 39, Year 2: 58) and *A. nipalensis* (Year 1: 52, Year 2: 45) detected were similar across the two years. The number of *R. undulatus* detected across two years varied (Year 1: 521, Year 2: 100). We did not detect spatial autocorrelation in hornbill detections in all the analyses for individual species except for the *A. nipalensis* in Year 2 (Supporting information). *Rhyticeros undulatus* encounter rate was consistently higher in patches where canopy food plants were present (Fig. 2 and Supporting information). We did not detect any association between encounter rates of the *B. bicornis* and *A. nipalensis* with the three types of food plants in the two years (Supporting information).

### Relationship between seed arrival and hornbill encounter rate

In plots where dispersed seeds were detected, the mean ( $\pm$  SD) number of seeds that were found in a plot were similar across the two years (Year 1: 1.32 ( $\pm$  1.1) seeds per plot; Year 2: 1.29 ( $\pm$  1) seeds per plot) pointing towards scatter dispersal of seeds. The mean ( $\pm$  SE) arrival rate of dispersed seeds of the five focal large-seeded species in the 24 patches was similar across the two years (Year 1: 32.1 ( $\pm$  6.1) seeds day<sup>-1</sup> ha<sup>-1</sup>, Year 2: 23.4 ( $\pm$  6.5) seeds day<sup>-1</sup> ha<sup>-1</sup>). Across the 24 patches, seed arrival rates varied between 6 and 116 seeds day<sup>-1</sup> ha<sup>-1</sup> in Year 1 and between 2 and 127 seeds day<sup>-1</sup> ha<sup>-1</sup> in 2011–2012. Seed arrival rates were positively associated

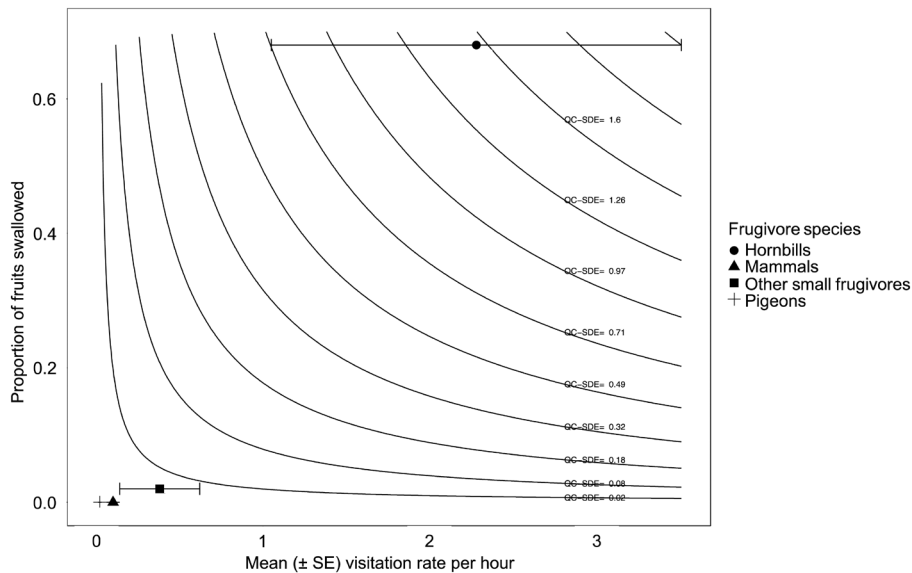


Figure 1. Seed dispersal effectiveness landscape showing the mean ( $\pm$  SE) visitation rates of different groups of frugivores on x-axis and proportion of fruits swallowed on the y-axis. The different kinds of frugivores includes hornbills (*Buceros bicornis*, *Rhyticeros undulatus* and *Aceros nipalensis*), mammals (primates and squirrels), other small frugivores (including barbets, hill mynas and cochoas) and pigeons (including imperial and wood pigeons) that were recorded during fruit tree censuses in Namdapha Tiger Reserve.

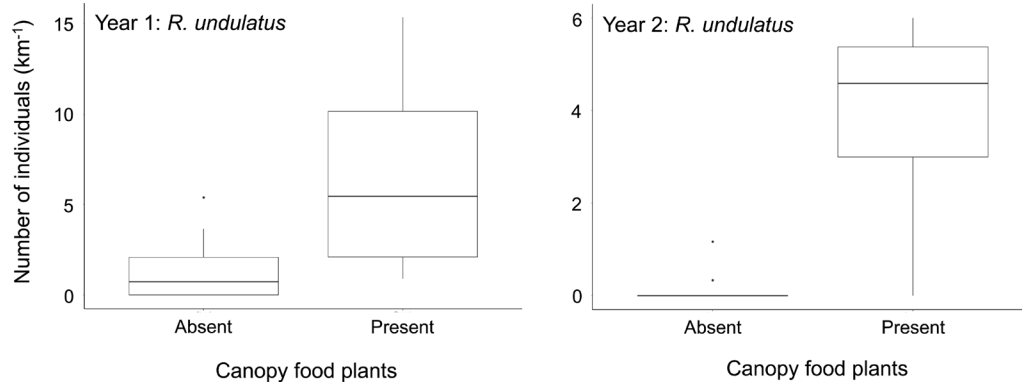


Figure 2. Encounter rate of *Rhyticeros undulatus* in patches with and without canopy food plants. Figures have been shown here only for relationships where 95% CI on estimated coefficients not overlapping zero. Supporting information for additional details.

with the overall hornbill encounter rates across the years (Table 2, Fig. 3). While the raw data of seed arrival exhibited spatial autocorrelation in Year 2 (Supporting information), the inclusion of hornbill encounter rate as the predictor weakened the strength of spatial autocorrelation in the seed arrival (Supporting information). Patches that experienced high scatter-dispersed seed rain in Year 1 also experienced high scatter-dispersed seed rain in Year 2 ( $r=0.69$ , 95% CI: 0.40–0.86).

### Seed removal

While there was variation in seed removal rates of scatter-dispersed seeds, the rates were generally low for the three large-seeded species (Fig. 4). Even after 100 days, the median removal rates were less than one for *Alseodaphne* and *Canarium* seeds, pointing towards very low mortality in the scatter-dispersal scenario (Fig. 4).

### Recruits

Overall mean ( $\pm$  SE) abundance of recruits (10–150 cm) of *B. assamica* ( $1312 \pm 207$  ha<sup>-1</sup>) was highest, followed by *Phoebe* sp. ( $207 \pm 88$  ha<sup>-1</sup>), *Dysoxylum* sp. ( $110 \pm 33$  ha<sup>-1</sup>) and *C. strictum* ( $1.2 \pm 0.8$  ha<sup>-1</sup>). Across the 22 sampling units, the species richness of recruits (of the four focal species, *C. strictum*, *Phoebe* sp., *Dysoxylum* sp. and *B. assamica*) varied from one to four species that were sampled. The diversity of seedlings and saplings was higher in patches that had canopy food plants (Fig. 5) but not in patches that had the presence of figs or had a higher abundance of middle-storey food plants (Supporting information).

## Discussion

In this study, we found a positive association between the abundance of canopy food plants and the hyperabundant *R. undulatus*. The overall hornbill abundance influenced the spatial distribution of scatter-dispersed seeds. While it is difficult to track the fate of seeds till adulthood, we found very low removal rates of scatter-dispersed seeds, and we found that the diversity of recruits was likely influenced through canopy food plants that influenced hornbill distribution. Our study highlights the crucial role of the rare canopy food plants and abundant hornbills in the system. Such landscapes with abundant hornbills and their food plants spread over vast areas are increasingly rare. Our study underscores the need to conserve these forests and the hornbills, which are indeed gardeners of these forests.

### Spatially contagious seed dispersal

Given the diverse array of frugivores and fleshy-fruited plants in tropical forests, it is relatively difficult to identify the role of particular frugivores in influencing spatially contagious dispersal. By focusing on a few large-seeded plants that hornbills mainly disperse, we could discern the role of hornbills in spatially contagious dispersal of select large-seeded trees that are dispersed mainly by hornbills. Previous studies have documented spatially contagious seed dispersal by determining seed arrival rates under heterospecific fruiting trees (Clark et al. 2004, Kwit et al. 2004, Viswanathan et al. 2015) or at preferred non-foraging sites (Wenny and Levey 1998, Russo and Augspurger 2004, Fedriani and Wiegand 2014) or by recording spatial variation in seed rain (Wright et al.

Table 2. Coefficients and associated 95% bootstrap confidence intervals for the GLM (with negative-binomial exponential structure) examining the relationship between seed arrival and encounter rates of the three large hornbill species that were the main dispersers of these large seeds across two years. The correlation coefficients of the observed and model-predicted values are also outlined. Pseudo  $R^2$  was calculated as  $1 - (\text{residual deviance}/\text{null deviance})$ .

	Intercept (bootstrap 95% CI)	Hornbill encounter rate (bootstrap 95% CI)	Model fit (observed versus predicted) $r$ (95% CI)	Pseudo $R^2$
Year 1	3.10 (2.70–3.53)	0.11 (0.01–0.34)	0.61 (0.28–0.82)	0.27
Year 2	2.42 (1.92–2.99)	0.32 (0.16–0.46)	0.72 (0.45–0.87)	0.38

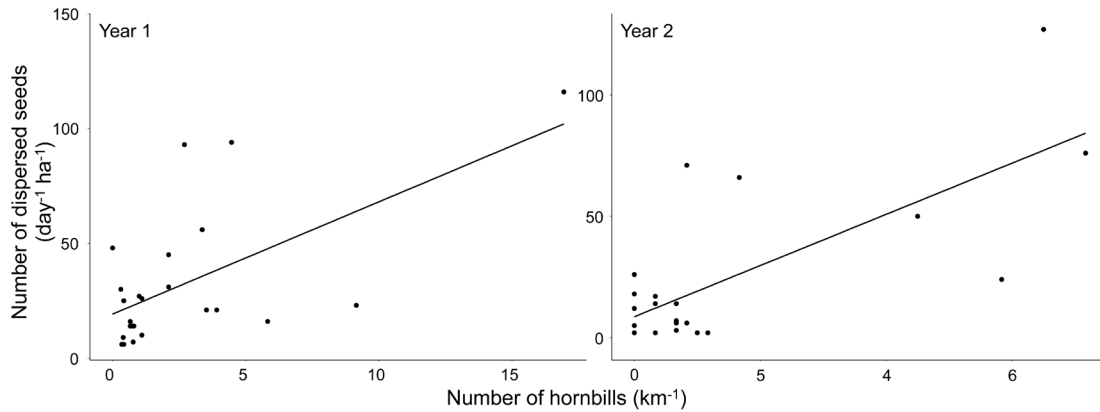


Figure 3. Relationship between the combined hornbill encounter rate (*Buceros bicornis*, *Rhyticeros undulatus* and *Aceros nipalensis*) and the net arrival of scatter-dispersed seeds across the two sampling years.

2016). By exploring multiple stages of the seed dispersal cycle, our study demonstrates how the distribution of food plants can influence the distribution of some frugivores, and how the frugivores can cause spatially contagious seed dispersal at the patch scale (1 ha) by exploring multiple stages of the seed dispersal cycle. We found consistency in spatial patterns of seed arrival, with similar sites receiving similar levels of seed rain in consecutive years. The relatively low seed removal rates of scatter-dispersed seeds and the high diversity of recruits in patches with a high incidence of canopy food plants point to the positive feedback between hornbills and their food plants, as speculated by Lázaro et al. (2005). The low seed removal rate of seeds post dispersal highlights that

the initial template of seed dispersal laid down by hornbills may have a strong bearing on the eventual recruitment patterns of these seeds.

### Is there rare-biased seed dispersal in the landscape?

Rare-biased seed dispersal is a phenomenon characterized by the disproportionate representation of seeds of rare species in seed rain, thereby contributing to the maintenance of tree diversity in the tropics (Carlo and Morales 2016). Interestingly, across both years, relatively rare tree species contributed the highest numbers of large seeds in our seed arrival plots (Supporting information). While this may be partially explained by the stature of the trees, with canopy

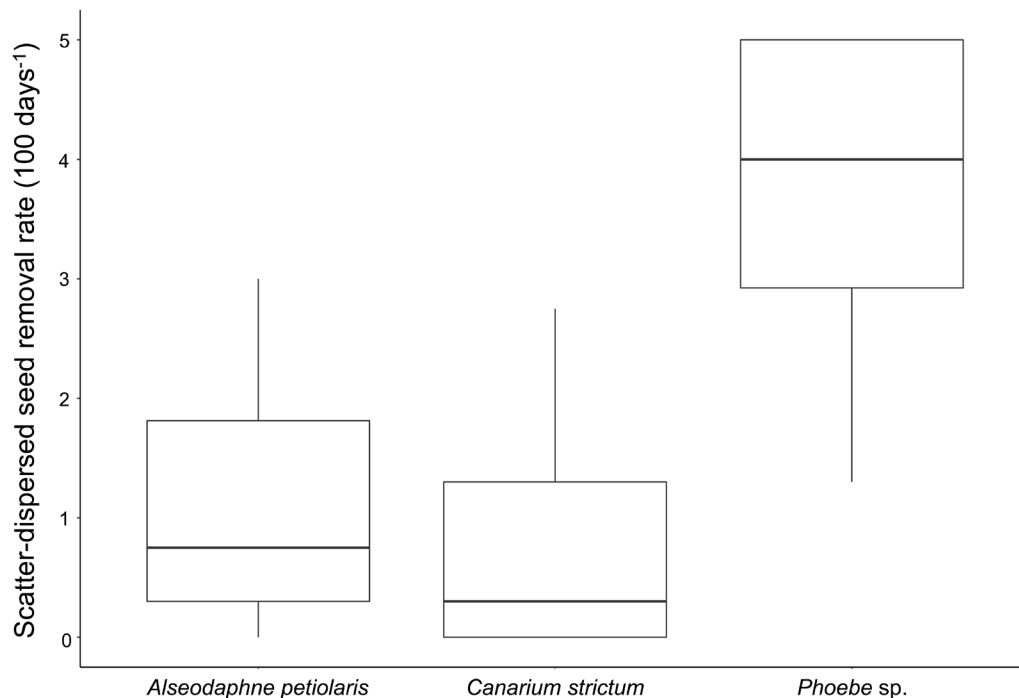


Figure 4. Seed removal rate (per plot per 100 days) for three large-seeded species of hornbill food plants *Alseodaphne petiolaris*, *Canarium strictum* and *Phoebe* sp. Each plot had five seeds to mimic the scatter-dispersal scenario.

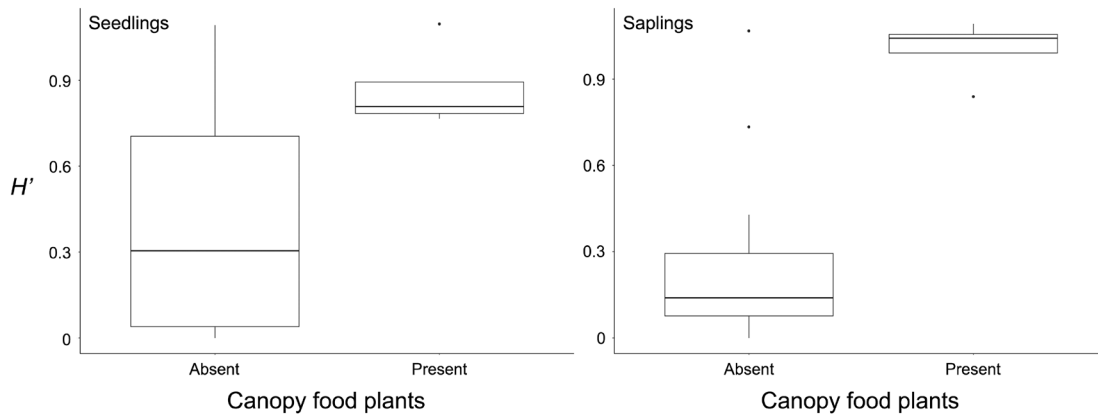


Figure 5. Diversity (Shannon–Weiner diversity measure) of seedlings (10–30 cm) and saplings (31–150 cm) in the 22 one-ha patches with and without canopy food plants.

food plants having much larger fruit crops than the middle-storey food plants (Naniwadekar et al. 2015c), there is also some indication of rare-biased seed dispersal. For example, *B. assamica* trees were 62 times more abundant as compared to *C. strictum* (Supporting information), but maximum fruit crop sizes recorded of *Canarium* were only 16 times higher as compared to *Beilschmiedia* (Naniwadekar et al. 2015c). Yet, *Canarium* seeds were almost twice as common compared to *Beilschmiedia*. Thus, despite *Beilschmiedia* fruits being far more common than *Canarium*, there was a higher representation of *Canarium* seeds in the seed arrival plots. We observed a similar pattern in the second year with *Phoebe* and *Beilschmiedia*. Canopy food plants like *C. strictum* are among the most preferred food plant species of the numerically abundant *R. undulatus* (Naniwadekar and Datta 2013, Naniwadekar et al. 2015c). In Year 2, *R. undulatus* were restricted to patches with canopy food plants indicating the potentially anti-apostatic selection of fruits and the consequent rare-biased seed dispersal, an aspect that needs to be explored in greater detail in the future (Allen and Weale 2005, Carlo and Morales 2016). A community-wide study of adult tree abundance of different fleshy-fruited plants, their fruit crops and seed arrival rates is required to confirm rare-biased seed dispersal in the landscape.

The disproportionate role of different kinds of fleshy-fruited plants in influencing seed dispersal at the patch scale is relatively less explored. Despite their relative rarity, canopy food plants emerged as important predictors of encounters of the commonest hornbill in the landscape. Patches with canopy food plants had a higher diversity of seedlings and saplings, suggesting their role in attracting frugivores, thereby contributing to plant diversity.

Unfortunately, canopy food plants like *Canarium* and *Phoebe* are heavily logged (often illegally) outside protected areas as they are important timber species (Naniwadekar et al. 2015a). *Canarium* trees are also heavily tapped for their resin, often resulting in adult tree mortality. Even inside the protected area, we did not find a *Canarium* tree that had not been tapped for its resin (Supporting information). Every year *R. undulatus* (Supporting information) migrate to the

mid- and high-elevations of Namdapha Tiger Reserve from the adjoining lowland forests in Arunachal Pradesh and Myanmar during the non-breeding season (Naniwadekar and Datta 2013). Their visit to these areas coincides with the peak in fruit availability in the mid-elevations, and fruits of canopy food plants like *Canarium* and *Phoebe* form a significant part of their diets (Naniwadekar et al. 2015c). Loss of these trees can permanently disrupt these intricate mutualisms that contribute to the maintenance of plant diversity in these forests.

### Fruit resource tracking by hornbills

Frugivores are known to track fruit resources at multiple scales (García and Ortiz-Pulido 2004, Naniwadekar et al. 2015c). In our study site, sympatric hornbills track fruit resources at different scales (Naniwadekar et al. 2015c). *B. bicornis* and *A. nipalensis* track trees with large fruit crop sizes while *R. undulatus* track resources at the landscape scale by seasonally visiting the middle-elevation forests of Namdapha Tiger Reserve (Naniwadekar et al. 2015c). *R. undulatus* were present in higher numbers in patches where their preferred canopy food plants were present. This was particularly evident in the second year, when *R. undulatus* were mostly seen in patches that had canopy food plants. However, we did not record such patterns for the *B. bicornis* and *A. nipalensis*, which typically range over shorter distances than the *R. undulatus* (Tifong et al. 2007, Naniwadekar et al. 2019b). Tracking resources at different scales likely allows these sympatric species to co-occur; this aspect needs to be explored in greater detail at sites that have more diverse assemblages of sympatric hornbills and frugivores to determine the relative role of niche packing and niche expansion in the assembly of frugivore communities (Pigot et al. 2016). Additionally, we only enumerated food plants (instead of fruit crops) in belt transects. Future work that explicitly estimates fruit crops of different fruit species might provide additional insights into hornbill resource tracking.

### Role of hornbills in seed dispersal

By focusing on a few large-seeded plants that hornbills primarily disperse, we could discern the role of hornbills in governing



the spatial distribution of large seeds, thereby potentially influencing the diversity of saplings of large-seeded plant species in the landscape. Hornbills are the largest avian frugivores and feed on a significantly higher number of fruits than other avian frugivores, and disperse seeds at large distances from the parent plants (Lenz et al. 2011, Naniwadekar et al. 2019a, b, 2021a). Our study found hornbills to be the most reliable seed dispersers of the focal large-seeded plants. With up to 12 700 large seeds dispersed per day per km<sup>2</sup> in patches with high hornbill abundances, the significant quantitative role potentially played by hornbills in the dispersal of large seeds was evident. Such estimates of the quantitative contribution of hornbills to seed dispersal in forests are not available in the literature. Previous studies have observed clumped-dispersal of seeds by hornbills under nest and roost trees with consequent poor regeneration of plants due to density-dependent mortality factors and unfavourable microhabitat conditions (Kinnaird 1998, Datta 2001, Kitamura et al. 2008). Our study demonstrates that hornbills also scatter disperse large quantities of seeds during their daily foraging with low predation rates of the scatter-dispersed seeds than under the parent trees (Viswanathan 2012) showing their effectiveness as seed dispersers. Additionally, a small proportion of seeds (<10%) are dispersed by male hornbills at the nest and roost sites (Naniwadekar et al. 2019b, 2020), emphasizing the predominant role of hornbills as scatter dispersers of seeds in tropical forests.

Places where these large-bodied hornbills occur sympatrically in such large densities are very few across the entire range of hornbills in Asia. Hornbills are hunted across their range, often leading to their local extirpation or drastic reductions in their populations (Bennett et al. 1997, Naniwadekar et al. 2015b). Hornbill habitats are getting modified due to logging pressures and habitat conversion, negatively affecting the abundance of their food plants (Naniwadekar et al. 2015a, Sheth et al. 2020). Disruptions in populations of hornbills and/or their food plants would disrupt this vital interaction necessary for the maintenance of tree diversity. Hornbills, particularly the *R. undulatus* (Supporting information), range over large areas searching for patchily distributed fruit resources (Keartumsom et al. 2011, Naniwadekar et al. 2019b). *Rhyticeros undulatus* do not breed in Namdapha, though the area is large (Naniwadekar and Datta 2013). They arrive in large numbers (up to 68 birds per km<sup>2</sup>) in the middle-elevation forests of Namdapha in the non-breeding season from the neighbouring lower elevation areas and numbers decline in the breeding season (Naniwadekar and Datta 2013). The spectacle of very high hornbill densities one witnesses in Namdapha is tied to the persistence of hornbills and their habitats. The phenomenon of spatially contagious seed dispersal driven by hornbills is critical for the maintenance of tree diversity. This needs to be recognized in conservation action and management planning to ensure that such important interactions are not lost.

**Acknowledgements** – We thank Navendu Page and Dr Haridasan for help with plant identification. We thank Ushma Shukla, Ashwin

Viswanathan and our field staff Duchayeh Yobin, Akhi Nathany, Ngwazakhi Yobin, Ngwayotse Yobin, Michepho Yobin, Tuchet Mossang, Manchet Mossang and Putol Singh for assistance in field. We are grateful to Japang Pansa and Phupla Singpho for their support in Miao. We thank M. D. Madhusudan, Jahnvi Joshi, Kulbhushansingh Suryawanshi, Soumya Prasad and Raman Kumar for valuable discussions. We thank Kim McConkey, Anna Traveset, Anand Osuri, Hari Sridhar, Abhishek Gopal, Geetha Ramaswami, Abir Jain and Arpitha Jayanth for valuable comments on the manuscript. We thank Dr Tomas Carlo and five anonymous reviewers for their detailed comments that helped improve the manuscript.

**Funding** – This study was funded by Rufford Small Grants, International Foundation of Science and Critical Ecosystem Partnership Fund. R. Naniwadekar was supported by grants from the Critical Ecosystem Partnership Fund, International Foundation for Science and Rufford Foundation. Nature Conservation Foundation provided logistical support in the field and in Bangalore.

**Permits** – We thank Arunachal Pradesh Forest Department for giving us the necessary permission (no. CWL/G/13(17)06-07/Pt-III/4219-32).

## Author contributions

**Rohit Naniwadekar:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead). **Charudutt Mishra:** Conceptualization (supporting); Formal analysis (supporting); Supervision (supporting); Writing – review and editing (supporting). **Kavita Isvaran:** Conceptualization (supporting); Formal analysis (supporting); Supervision (supporting); Writing – review and editing (supporting). **Aparajita Datta:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Resources (supporting); Supervision (lead); Writing – review and editing (lead).

## Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02748>>.

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.qrfj6q5gq>> (Naniwadekar et al. 2021b).

## References

- Allen, J. A. and Weale, M. E. 2005. Anti-apostatic selection by wild birds on quasi-natural morphs of the land snail *Cepaea hortensis*: a generalised linear mixed models approach. – *Oikos* 108: 335–343.
- Bennett, E. L., Nyaoi, A. J. and Sompud, J. 1997. Hornbills *Buceros* spp. and culture in northern Borneo: can they continue to co-exist? – *Biol. Conserv.* 82: 41–46.
- Carlo, T. A. and Morales, J. M. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. – *Ecology* 97: 1819–1831.

- Chanthorn, W., Wiegand, T., Getzin, S., Brockelman, W. Y. and Nathalang, A. 2018. Spatial patterns of local species richness reveal importance of frugivores for tropical forest diversity. – *J. Ecol.* 106: 925–935.
- Clark, C. J., Poulsen, J. R., Connor, E. F. and Parker, V. T. 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. – *Oecologia* 139: 66–75.
- Datta, A. 2001. An ecological study of sympatric hornbills and fruiting patterns in a tropical forest in Arunachal Pradesh. – PhD thesis, Saurashtra Univ., Gujarat, India.
- Datta, A. and Rawat, G. S. 2003. Foraging patterns of sympatric hornbills during the nonbreeding season in Arunachal Pradesh, northeast India. – *Biotropica* 35: 208–218.
- Fedriani, J. M. and Wiegand, T. 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. – *Ecology* 95: 514–526.
- García, D. and Ortiz-Pulido, R. 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. – *Ecography* 27: 187–196.
- Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. – *Oecologia* 79: 417–426.
- Jackman, S. 2020. pscl: Classes and methods for R developed in the Political Science Computational Laboratory. United States Studies Centre, Univ. of Sydney, Sydney, NSW, Australia. – R package version 1.5.5, <<https://github.com/atahk/pscl/>>.
- Jordano, P. 2000. Fruits and frugivory. – In: Fener, M. (ed.), *Seeds: the ecology of regeneration in plant communities*. CABI Publishing, Wallingford, pp. 125–166.
- Jordano, P. 2014. An R package for plots of effectiveness landscapes in mutualisms: effect.lndsc. . – <<https://doi.org/10.5281/zenodo.376763>>.
- Keartumsom, Y., Chimchome, V., Poonswad, P., Pattanavibool, A. and Pongpattananurak, N. 2011. Home range of great hornbill (*Buceros bicornis* Linnaeus, 1758) and wreathed hornbill (*Rhyticeros undulatus* (Shaw) 1881) in non-breeding season at Khao Yai National Park, Nakhon Ratchasima Province. – *J. Wildl. Thailand* 18: 47–55.
- Kinnaird, M. F. 1998. Evidence for effective seed dispersal by the sulawesi red-knobbed hornbill, *Aceros cassidix*. – *Biotropica* 30: 50–55.
- Kinnaird, M. and O'Brien, T. G. 2007. The ecology and conservation of asian hornbills: farmers of the forest. – Univ. of Chicago Press.
- Kinnaird, M. F., O'Brien, T. G. and Suryadi, S. 1996. Population fluctuation in sulawesi red-knobbed hornbills: tracking figs in space and time. – *Auk* 113: 431–440.
- Kitamura, S., Yumoto, T., Noma, N., Chuailua, P., Maruhashi, T., Wohandee, P. and Poonswad, P. 2008. Aggregated seed dispersal by wreathed hornbills at a roost site in a moist evergreen forest of Thailand. – *Ecol. Res.* 23: 943–952.
- Kwit, C., Levey, D. J. and Greenberg, C. H. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. – *Oikos* 107: 303–308.
- Lázaro, A., Mark, S. and Olesen, J. M. 2005. Bird-made fruit orchards in northern Europe: nestedness and network properties. – *Oikos* 110: 321–329.
- Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B. H., Wikelski, M. and Böhning-Gaese, K. 2011. Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. – *Proc. R. Soc. B* 278: 2257–2264.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. – *Nature* 403: 853–858.
- Naniwadekar, R. and Datta, A. 2013. Spatial and temporal variation in hornbill densities in Namdapha Tiger Reserve, Arunachal Pradesh, north-east India. – *Trop. Conserv. Sci.* 6: 734–748.
- Naniwadekar, R., Shukla, U., Isvaran, K. and Datta, A. 2015a. Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest. – *PLoS One* 10: e0120062.
- Naniwadekar, R., Mishra, C., Isvaran, K., Madhusudan, M. D. and Datta, A. 2015b. Looking beyond parks: the conservation value of unprotected areas for hornbills in Arunachal Pradesh, eastern Himalaya. – *Oryx* 49: 303–311.
- Naniwadekar, R., Mishra, C. and Datta, A. 2015c. Fruit resource tracking by hornbill species at multiple scales in a tropical forest in India. – *J. Trop. Ecol.* 31: 477–490.
- Naniwadekar, R., Chaplod, S., Datta, A., Rathore, A. and Sridhar, H. 2019a. Large frugivores matter: insights from network and seed dispersal effectiveness approaches. – *J. Anim. Ecol.* 88: 1250–1262.
- Naniwadekar, R., Rathore, A., Shukla, U., Chaplod, S. and Datta, A. 2019b. How far do Asian forest hornbills disperse seeds? – *Acta Oecol.* 101: 103482.
- Naniwadekar, R., Rathore, A., Shukla, U. and Datta, A. 2020. Patterns of roost site use by Asian hornbills and implications for seed dispersal. – *bioRxiv*: 2020.09.01.277608.
- Naniwadekar, R., Gopal, A., Page, N., Ghuman, S., Ramachandran, V. and Joshi, J. 2021a. Large frugivores matter more on an island: Insights from island–mainland comparison of plant–frugivore communities. – *Ecol. Evol.* 11: 1399–1412.
- Naniwadekar, R., Mishra, C., Isvaran, K. and Datta, A. 2021b. Data from: Gardeners of the forest: hornbills govern the spatial distribution of large seeds. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.qrfj6q5gq>>.
- Paradis, E. and Schliep, K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in {R}. – *Bioinformatics* 35: 526–528.
- Pigot, A. L., Trisos, C. H. and Tobias, J. A. 2016. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. – *Proc. R. Soc. B* 283: 20152013.
- Poonswad, P., Kemp, A. and Strange, M. 2013. Hornbills of the world: a photographic guide. – Draco Publishing.
- Russo, S. E. and Augspurger, C. K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. – *Ecol. Lett.* 7: 1058–1067.
- Schupp, E., Milleron, T. and Russo, S. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. – In: Levey, D. J., Silva, W. R. and Galetti, M. (eds), *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing, pp. 19–33.
- Sheth, C., Datta, A. and Parashuram, D. 2020. Persistent loss of biologically-rich tropical forests in the Indian eastern Himalaya. – *Silva Fenn.* 54: 10373.
- Tifong, J., Chimchome, V., Poonswad, P. and Pattanavibool, A. 2007. Home range and habitat use of rufous-necked hornbill *Aceros nipalensis* by radio tracking in Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani Province. – *Thailand J. For.* 26: 28–39.
- Trolliet, F., Forget, P.-M., Doucet, J.-L., Gillet, J.-F. and Hambuckers, A. 2017. Frugivorous birds influence the spatial organization of tropical forests through the generation of seedling recruitment foci under zoochoric trees. – *Acta Oecol.* 85: 69–76.
- Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S. – Springer.

- Viswanathan, A. 2012. Seed dispersal by avian frugivores: non-random heterogeneity at fine scales. – MSc thesis, Tata Inst. for Fundamental Research (TIFR), Mumbai, India.
- Viswanathan, A., Naniwadekar, R. and Datta, A. 2015. Seed dispersal by avian frugivores: non-random heterogeneity at fine scales. – *Biotropica* 47: 77–84.
- Wenny, D. G. and Levey, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. – *Proc. Natl Acad. Sci. USA* 95: 6204–6207.
- Wenny, D. G., Şekercioğlu, Ç. H., Cordeiro, N. J., Rogers, H. S. and Kelly, D. 2016. Seed dispersal by fruit-eating birds. – In: Şekercioğlu, Ç. H. et al. (eds), *Why birds matter?* Univ. of Chicago Press, pp. 107–146.
- Wright, S. J., Calderón, O., Hernández, A., Detto, M. and Jansen, P. A. 2016. Interspecific associations in seed arrival and seedling recruitment in a Neotropical forest. – *Ecology* 97: 2780–2790.
- Zeileis, A., Kleiber, C. and Jackman, S. 2008. Regression models for count data in R. – *J. Stat. Softw.* 27: 1–25.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R.* – Springer.