

Recruitment of Hornbill-Dispersed Trees in Hunted and Logged Forests of the Indian Eastern Himalaya

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Abstract: *Hunting of hornbills by tribal communities is widespread in logged foothill forests of the Indian Eastern Himalaya. We investigated whether the decline of hornbills has affected the dispersal and recruitment of 3 large-seeded tree species. We hypothesized that 2 low-fecundity tree species, *Chisocheton paniculatus* and *Dysoxylum binectariferum* (Meliaceae) bearing arillate fruits, are more dispersal limited than a prolifically fruiting drupaceous tree *Polyalthia simiarum* (Annonaceae), which has potential dispersers other than hornbills. We estimated the abundance of large avian frugivores during the fruiting season along transects in 2 protected and 2 disturbed forests. We compared recruitment of the tree species near (<10 m) and far (10–40 m) from parent trees at protected and disturbed sites. Median abundance of Great (Buceros bicornis), Wreathed (Aceros undulatus), and Oriental Pied Hornbills (Anthracoceros albirostris) were significantly lower in disturbed forests, but sites did not differ in abundances of the Mountain Imperial Pigeon (Ducula badia). Overall, tree species showed more severely depressed recruitment of seedlings (77% fewer) and juveniles (69% fewer) in disturbed than in protected forests. In disturbed forests, 93% fewer seedlings of *C. paniculatus* were beyond parental crowns, and a high number of all seedlings (42%) accumulated directly under reproductive adults. In contrast, *D. binectariferum* and *P. simiarum* were recruitment rather than dispersal limited, with fewer dispersed seedlings surviving in disturbed than in protected forests. Results are consistent with the idea that disturbance disrupts mutualisms between hornbills and some large-seeded food plants, with the caveat that role redundancy within even small and specialized disperser assemblages renders other tree species less vulnerable to loss of regular dispersal agents.*

Keywords: dispersal limitation, eastern Himalaya, ecological redundancy, hornbills, hunting, India, recruitment limitation, tropical rain forest

Reclutamiento de Árboles Dispersados por Cálaos en Bosques con Cacería y Tala en Himalaya Oriental Hindú

Resumen: *La cacería de cálaos por comunidades tribales está muy extendida en bosques talados del Himalaya Oriental Hindú. Investigamos si la declinación de cálaos ha afectado la dispersión y el reclutamiento de tres especies de árboles con semillas grandes. Nuestra hipótesis fue que la dispersión de dos especies de árboles de baja fecundidad, *Chisocheton paniculatus* y *Dysoxylum binectariferum* (Meliaceae) con frutos arillados, era más limitada que la de un árbol con drupas *Polyalthia simiarum* (Annonaceae), que tiene dispersores potenciales diferentes a los cálaos. Estimamos la abundancia de aves frugívoras grandes durante la época de fructificación a lo largo de transectos en dos bosques protegidos y dos bosques perturbados. Comparamos el reclutamiento de las especies de árboles cerca (< 10m) y lejos (10–40 m) de los árboles padre en sitios protegidos y perturbados. La abundancia media de *Buceros bicornis*, *Aceros undulatus* y *Anthracoceros albirostris* fue significativamente menor en los bosques perturbados, pero los sitios no tuvieron diferencias en la abundancia de *Ducula badia*. En general, las especies de árboles mostraron un reclutamiento de plántulas (77% menos) y juveniles (69% menos) severamente deprimido en los bosques perturbados. En los bosques*

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perturbados, 93% menos plántulas de C. paniculatus se encontraron más allá de las coronas parentales, y un alto número de todas las plántulas (42%) se acumularon directamente debajo de los adultos reproductivos. En contraste, D. binectariferum y P. simiarum estuvieron limitados en reclutamiento en lugar de dispersión, con menor supervivencia de plántulas dispersadas en los bosques perturbados que en los protegidos. Los resultados son consistentes con la idea de que la perturbación interrumpe mutualismos entre cálaos y algunas plantas con semillas grandes, con la advertencia de que la redundancia de papeles en ensamblajes pequeños de dispersores especializados hace que otras especies de árboles sean menos vulnerables a la pérdida de sus agentes dispersores.

Palabras Clave: bosque tropical lluvioso, cacería, cálaos, Himalaya Oriental, India, limitación en el reclutamiento, limitación en la dispersión, redundancia ecológica

Introduction

Habitat alteration and degradation are rampant throughout the tropics and may have severe consequences for the key plant–animal mutualisms of pollination and seed dispersal. The contribution of hunting, forest fragmentation, and logging to the defaunation of local biotas is well documented (Redford 1992; Peres & Palacios 2007). Large-bodied vertebrates are particularly vulnerable to extinction due to their large home ranges, small population sizes, low reproductive rates, and declining foraging opportunities (Warburton 1997; Renjifo 1999) and because they are the preferred prey of human hunters (Bodmer et al. 1997). What remains unclear is the manner in which such vertebrate declines alter the subtle interplay of seed dispersal and postdispersal seed predation, and the seedling predation and herbivory that determine regeneration of tree species (e.g., Stoner et al. 2007; Wright et al. 2007). A key question is the degree to which animal-dispersed trees depend on dispersers (Howe 1977). For instance, do large-seeded trees suffer poor dispersal and recruitment because of the loss of large-bodied seed dispersers (Peres & Roosmalen 2002) or does role redundancy among frugivores buffer some trees against disperser loss (Moore & Swihart 2007)? We evaluated the consequences of population declines of large-bodied hornbills on the regeneration of their large-seeded tree mutualists in foothill forests of the Eastern Himalaya.

Frugivorous animals promote seedling recruitment by helping seeds escape high density-dependent mortality near parent trees; they move seeds to special microsites favorable for establishment or carry seeds to open habitats (Janzen 1970; Connell 1971; Howe & Smallwood 1982). At our sites in the eastern Himalaya, hornbills disseminate seeds of over 25% of the trees and are thought to be the primary dispersal agents for large-seeded trees in the families Meliaceae, Myristicaceae, and Lauraceae (Datta 2001). Whether effective reproduction is compromised by absence of particular dispersal agents on which animal-dispersed trees appear to depend is unknown.

Large seeds are consumed by few potential dispersers. Because only large birds with large gape widths can transport large seeds (Wheelwright 1985), we expected large-seeded trees relying on declining populations of large birds to be most dispersal limited and therefore vulnerable to loss of particular dispersal agents (Wang & Smith 2002). Here we define *dispersal limitation* as recruitment failure because seeds do not arrive at potential recruitment sites. Recruitment may also fail for other reasons if dispersed seeds die due to factors such as high seed or seedling predation, altered abiotic regimes, or simply low seed set. Sometimes hidden in the concern over dispersal limitation due to loss of dispersal agents are 2 realities: many trees have redundant disperser assemblages (see Moore & Swihart 2007) and many if not most trees recruit poorly for reasons other than absence of dispersers (Clark et al. 2007). We recognize the need to distinguish whether poor recruitment results from loss of dispersers or from other factors that may also limit recruitment.

Plants visited by many fruit-eating animals are more likely to have redundant disperser assemblages because some seed vectors may compensate for the loss of those that are hunted. These dispersers may increase in abundance following the extirpation of ecologically similar competitors or change their behavior by removing more seeds in disturbed than undisturbed sites (Loiselle & Blake 2002). Although cases of other species stepping in to perform equivalent functions are known from pollination mutualisms (Aizen & Feinsinger 1994; Dick et al. 2001), few examples exist in the seed-dispersal literature. It is still unknown whether alternative dispersal agents can maintain rough equivalence in the quantity and quality of seed dispersal (Schupp 1993) for tree species that have lost one or more seed vectors.

We hypothesize that 2 large-seeded tree species, *Chisocheton paniculatus* and *Dysoxylum binectariferum* (both Meliaceae), are dispersal and recruitment limited in hunted and logged areas. Several traits suggest their obligate reliance on few dispersers. Large seeds preclude dispersal by most birds other than large-bodied hornbills and Imperial Pigeons (*Ducula* spp.). Primates or

mammals are not known to disperse their fruits (Datta 2001; P.S., personal observation). Furthermore, low fecundity and long fruiting seasons with only a few fruits ripening at any one time suggest they depend on one or a few "reliable" dispersal agents, without which they may suffer from reduced dispersal and recruitment.

Conversely, the common, large-seeded, drupe-bearing tree *Polyalthia simiarum* (Annonaceae) is a fecund species that often fruits twice a year. It has more potential dispersal agents, including civets, primates (P.S., unpublished data), and bats (K. Kakati, personal communication). Although also relatively large seeded, its larger disperser assemblage suggests it relies less exclusively on hornbills for dispersal than the other species. Moreover, high fecundity and multiple fruiting seasons do not imply a narrowly restricted disperser assemblage. The species may be adapted to attract whatever fruit-eating animals are available in a given season.

We tested the prediction that loss of hornbills adversely impacts the dispersal and recruitment of those large-seeded species that most depend on them for seed dissemination. We asked whether abundances of large avian frugivores differed between protected and hunted forests when focal trees were fruiting. We determined whether hornbill-disseminated trees showed lower recruitment in disturbed sites due to dispersal failures or other factors. We compared seedling and juvenile tree densities under (<10 m) and away (10–40 m) from trees in protected and disturbed sites. High seedling and juvenile densities under adults, but not a few meters away, implies low seed dispersal, whereas low juvenile densities, but not seedling densities away from reproductive adults in disturbed sites, implies recruitment limitation from causes other than dispersal limitation.

Methods

Study Sites

Our study was conducted in 2 protected sites in Pakke Wildlife Sanctuary (PWS) (26°54'N–27°16'N, 92°36'–93°09'E; 862 sq. km) and 2 hunted and logged areas in adjoining Papum Reserve Forest (RF) (27°0'N, 93°10'E; 1064 km²) in East Kameng district of Arunachal Pradesh within the Eastern Himalayas. The 4 sites were in lowland, semi-evergreen foothill forests. Protected sites were in the west bank of Seijosa (26°56'N, 92°58'E) on the southeastern boundary of PWS bordering the Pakke River and forests near Khari (26°59' N, 92°54'E; approximately 11 km west of Seijosa near the southern boundary of PWS). In both sites prohibition of hunting was actively enforced. Two hunted sites were in the Papum RF of Khellong Forest Division that adjoins PWS on its eastern border. One hunted site (3) Lanka (27°01'N, 93°02'E) was approximately 14 km farther east of our first site (west

bank) and was separated from the sanctuary by the Pakke River. The second hunted site (4) was approximately 11 km southeast of Lanka (26°59' N, 93°07'E).

Prior to the sanctuary's declaration in 1977, all study sites were managed under Khellong Forest Division (Padmawathe et al. 2004). Study sites were comparable in geology, rainfall, climate, vegetation, and topography. Rainfall followed a bimodal pattern, with a southwestern monsoon May to September and short rains from the northeast monsoon in December to April, averaging 2506 mm (Birand & Pawar 2004). Study sites were hilly, with elevations ranging from 200 to 500 m. Elevations elsewhere in the sanctuary and adjoining forests extended up to 2000 m. The vegetation type was Assam Valley tropical semievergreen forest (Champion & Seth 1968). Datta & Rawat (2003) recorded 343 species of woody flowering plants in these forests, with a predominance of Euphorbiaceae and Lauraceae (Padmawathe et al. 2004). Additional details of vegetation and site are available (see Supporting Information). Protected and hunted sites were free of grazing by cattle or goats. Peripheral areas of PWS were commercially logged (Birand & Pawar 2004) until the late 1970s, but at the time of the study were free of logging. Forests were logged under a selection system in which trees were selectively felled and allowed to regenerate naturally (Sen 1978). The Supreme Court of India banned logging in 1996, but in many forests, logging continues.

Hunting hornbills for meat and ornamentation is a traditional practice in Arunachal. Nishi groups dominated the study area; one disturbed site also had a small population of Sulungs. Patrolling and community-enforced poaching bans have prevented hornbill hunting in protected sites. In disturbed sites tribes used indigenous traps and firearms to hunt. Traditional trapping has been carried out for centuries, whereas hunting with firearms has been practiced in the area for about 30 years.

Tree Species

The focal trees we examined were *D. binectariferum* and *C. paniculatus* (both Meliaceae) and *P. simiarum* (Annonaceae) (Table 1). *C. paniculatus* and *D. binectariferum* are short, midstory, evergreen species. *C. paniculatus* has polygamous flowers and dehiscent, red capsules with black seeds, partly enclosed by orange-white arillodes. *D. binectariferum* has bisexual flowers with orange, dehiscent capsular fruits and greenish-yellow seeds covered by black arils. Fruits take a long time to ripen, with only a few dehiscent at any point. *P. simiarum* is a taller, evergreen tree, with bisexual flowers and abundant drupes that change color from green to black when ripe.

Table 1. Characteristics of focal tree species: height, fruit and seed size, wet mass, contribution to hornbill diet, tree density, fruiting period, and seed predators.

Tree species	Mean tree height (m)(SE), n ^a	Mean fruit size (length × width × depth) (mm) (SE), n ^a	Mean seed size (length × width × depth) (mm) (SE), n (with aril) ^a	Seed wet mass (g) ^b	Contribution to hornbill diet (%) (no., biomass) ^{b,c}	Tree density in protected sites (trees/ha) ^b	Fruiting period ^{a,b}	Seed predators ^{a,b}
<i>Chisocobeton paniculatus</i>	13.01 (0.36) N = 97	60.98 (0.74) × 57.42 (1.62) × 54.49 (1.45), 45 fruits, 22 trees	31.4 (0.89) × 23.74 (0.74) × 19.3 (0.6), 102 seeds, 45 fruits, 22 trees ^d	12.12	3, 5	21.52	April–July (peak May–June)	rodents
<i>Dysoxylum binectariferum</i>	13.7 (0.7), 55	52.68 (0.73) × 49.63 (0.87) × 46.8 (0.85), 64 fruits, 21 trees	29.6 (0.32) × 21.96 (0.28) × 17.0 (0.25), 187 seeds, 64 fruits, 22 trees ^d	13.14	12, 22	4.19	February–May (peak March, April)	rodents
<i>Polyalthia simiarum</i>	31.08 (0.74), 37	28.9 (0.97) × 19.9 (0.49) × 17.0, (0.46), 40 fruits, 11 trees ^d	-	4.94	56, 50	20.76	May–July; also December–February	beetles

^aSource: this study.

^bSource: Datta (2001).

^cDuring the breeding season.

^dPart of fruit removed by dispersers: seed with aril for capsular species and single-seeded drupe for *P. simiarum*.

Avian Dispersers

Three hornbill species (Bucerotidae), the Great Indian Hornbill (*Buceros bicornis*), Oriental Pied Hornbill, (*Anthracoceros albirostris*), Wreathed Hornbill (*Aceros undulatus*), and Mountain Imperial Pigeon (*Ducula badia*) dispersed seeds from our tree species. The Green Imperial Pigeon (*Ducula aenea*) also occurred at Pakke but was not observed during this study. Weights of the Great, Wreathed, and Oriental Hornbill and Imperial Pigeon are 2.2–3, 2–2.5, 0.7–0.8, and 0.5–0.6 kg, respectively (Kitamura et al. 2004). Gape widths of these species are approximately 122, 50, 36, and 26 mm, respectively (Datta 2001). Information on other frugivores (nondispersers) and megaherbivores, such as elephants and deer that do not appear to eat the seeds or seedlings of our focal tree species, are in Supporting Information.

Hornbill and *Ducula* Pigeon Abundance

We sought to determine whether protected and disturbed areas differed in the abundance of their large avian dispersers when focal tree species were in fruit, which corresponds to the hornbill breeding season when movement of breeding males is restricted (Poonswad & Tsuji 1994). We censused hornbills and *Ducula* pigeons in May and June 2006. Eight transects (4 each in protected and disturbed sites) were each walked 3 times (80 km total). Transect lengths were 3.5, 3.1, 4.25, and 4.57 km for the protected sites, and transects in the disturbed sites were 2.3, 2.5, and 3 km. At each site one transect spanned a riverine habitat and the second a forested tract. All birds seen perched or flying or heard up to approximately 200 m were recorded. We walked transects after sunrise at about 1 km/h. We compared the abundance (numbers encountered per kilometer) on a per day basis between sites. (For details of hornbill phenology see Supporting Information.)

Dispersal and Recruitment

To determine whether seed dispersal or recruitment suffered in disturbed sites, we counted seedlings (< 30 cm height) and juveniles (> 30–100 cm) under (< 10 m) and away (10–40 m) from focal trees. Seedlings were from the 2006 fruiting season, and juveniles were older than 1 year. We censused 10, randomly sampled, adult individuals per species at each site (120 trees total, 40 per species). We evaluated regeneration in single, randomly directed 20° wedge-shaped transects radiating 40 m from the base of each parent tree. Seedlings and juveniles were counted in 2-m intervals and then reclassified as those close to a parent (<10 m from the base of the trunk) or far from a parent (beyond 10 m). Trees were censused from October to December 2006. Parental crowns did not exceed a radius of 10 m.

Statistical Analyses

To determine whether hunted and protected sites differed in the abundances of large, frugivorous birds, we compared the encounter rate (numbers seen per kilometer) per day of each species with nonparametric Mann-Whitney tests.

We evaluated the consequences of differences in seed dispersal and recruitment in protected and disturbed areas by determining whether mean numbers of seedlings and juveniles (dependent variables) differed near (< 10 m) and far (10–40 m) from a tree as a function of habitat status with nested and crossed analysis of variance (ANOVA). We expected dispersal limitation to be reflected in far more undispersed seedlings under than away from adults because of low dispersal in disturbed sites and more seedlings to be dispersed away from adults in protected sites. Given that dispersal agents routinely fly farther than 40 m after visiting a tree, this is primarily a test of successful or unsuccessful removal of seeds from trees, as reflected by a significant interaction of habitat (protected or disturbed) with proximity to parental crowns for seedlings. Poor dispersal combined with high seedling densities under crowns might result in density-dependent mortality. If so, poor juvenile recruitment would accompany lower dispersal of seedlings and produce a significant interaction of habitat with distance from parents for juveniles. If species recruit poorly in disturbed sites due to reasons other than poor dispersal, however, this would cause a significant interaction of habitat with proximity to tree for juveniles, but not seedlings. That is, dispersers move seeds away from parent trees in hunted sites, but dispersed seedlings fail to survive, causing higher attrition of juveniles in disturbed sites than in protected ones.

Nested and crossed ANOVAs for the 3 species combined included the main, crossed factors of habitat (protected vs. hunted and logged), species of tree, and proximity to trees (near and far). Sites (2/habitat) were nested in habitat and trees were nested in site. Significant differences in the main ANOVAs were followed with individual species ANOVAs because post hoc tests were invalid with nested ANOVAs. For each individual species' ANOVA, habitat and proximity to tree were crossed, whereas sites were nested in habitat and trees were nested in site. Dependent variables were log transformed before analysis. Statistical analyses were performed with MINITAB (version 15.0, MINITAB 2007, MINITAB, Inc., State College, Pennsylvania) and SPSS (version 15.0, SPSS Software 2006, SPSS, Inc., Chicago, Illinois).

Results

Hornbill and Fruit Pigeon Abundance

Hornbills were much reduced at hunted sites during the fruiting season. Great Hornbills had all but disappeared

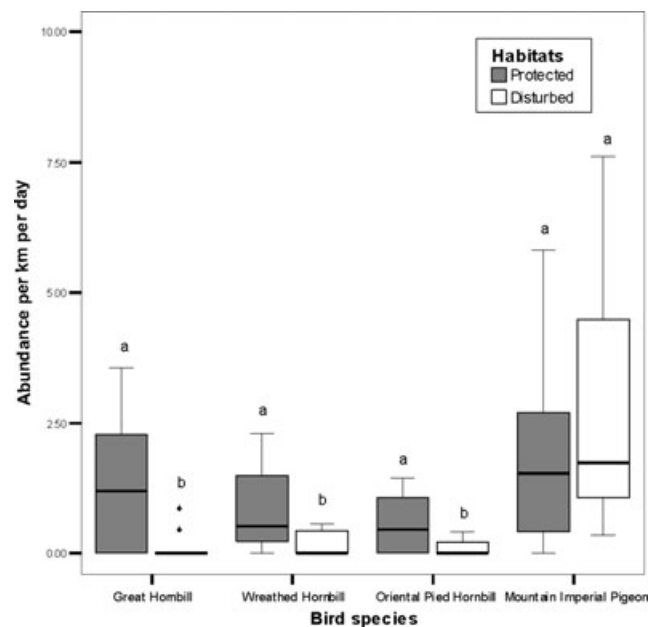


Figure 1. Median and one quartile encounter rate of bird species per day (number of individual birds per kilometer) in 2 protected and 2 disturbed forests. Box plots in a 2-way contrast with different letters are statistically different ($p < 0.05$ – 0.01); those with the same letters in a contrast are not significantly different ($p > 0.05$).

in disturbed compared with protected forests ($U = 31$, $p < 0.01$; median of 0 vs. 1.19). Similarly, the median abundance of Wreathed Hornbills ($U = 35$, $p < 0.05$; median 0 vs. 0.52) and Oriental Pied Hornbills ($U = 41.5$, $p < 0.05$; median 0 vs. 0.44) (Fig. 1) were both lower in disturbed sites. Protected and disturbed forests did not differ in the abundance of the Imperial Pigeons ($U = 53$, $p > 0.05$).

Our results remained consistent when we added census data for additional sites in which we did not sample tree recruitment. This included a spatially distant hunted site (Doimara Reserve Forest, Khellong Forest Division 27°00' N, 92°00' E) and protected site (located within PWS, 26°59' N, 93°00' E), raising the total distance walked to approximately 111 km in May–June 2006. Median abundances of Great (median 0 vs. 1.55), Wreathed (median 0 vs. 0.61), and Oriental Pied Hornbills (median 0 vs. 0.42) were again lower in hunted forests ($U = 43$, $p < 0.0001$; $U = 65$, $p < 0.005$; $U = 97$, $p < 0.05$), but sites did not differ in Imperial Pigeon abundances (median 1.22 vs. 0.97; $U = 131$, $p > 0.05$). Furthermore, data from 6 sites (2 hunted, 4 protected) collected from January to July 2008 confirmed that hornbill numbers remained low in hunted and logged areas over multiple years (P.S., unpublished data). These new findings, which showed substantial declines in hornbill abundances but not Imperial Pigeons, strongly buttress our 2006 results.

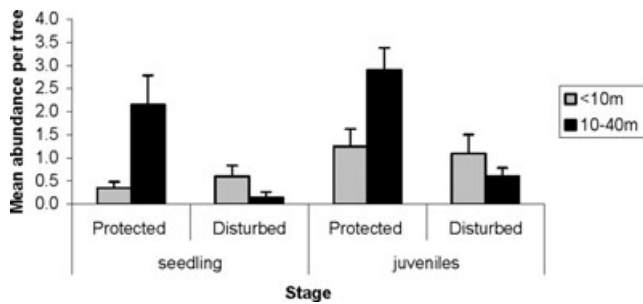


Figure 2. Mean (SE) seedling and juvenile recruits per tree as a function of distance from the tree and protection status of the area for *C. paniculatus* (Meliaceae). Untransformed data are presented. Analyses are from log-transformed data.

Tree Dispersal and Recruitment

Nested and crossed ANOVAS of the 3 tree species combined yielded no site effects independent of the protected versus hunting and logging distinction. Recruitment of all species was impaired in hunted and logged sites ($F_{1,2} = 24.28, p < 0.05$ for seedlings and $F_{1,2} = 433.81, p < 0.005$ for juveniles). Overall, fewer seedlings (77% fewer) and juveniles (69% fewer) recruited in hunted forests than protected ones. Over all species, protected sites had 77% higher juvenile recruitment away from the parents compared with disturbed ones ($F_{1,114} = 18.7, p < 0.0001$).

For *C. paniculatus* seedlings and juveniles, the interaction of habitats with distance from tree was highly significant ($F_{1,38} = 15.59, p < 0.0001$; $F_{1,38} = 10.49, p < 0.005$) and disturbed forests had far more (42%) undispersed seedlings under parental crowns than protected forests (Fig. 2). Conversely, the mean number of seedlings occurring > 10 m away in protected sites was 93% higher than in hunted forests. A correspondingly higher percentage of juveniles (79%) recruited away from trees in protected forests than disturbed ones. Dense aggregations of undispersed seeds and seedlings under parents in disturbed sites and poor juvenile recruitment were consistent with density-dependent thinning.

D. binectariferum seedlings appeared to be dispersed at all sites, but fewer juveniles recruited away from the tree in disturbed forests. There were 65% more seedlings in protected than disturbed forests ($F_{1,2} = 27.72, p < 0.05$), but the interaction of habitat with distance was not significant ($F_{1,38} = 0.01, p = 0.912$). Seedlings were equally abundant near and far from the tree in both habitats. For juveniles habitat was significant as was distance from the tree ($F_{1,2} = 32.17, p < 0.05, F_{1,38} = 4.89, p < 0.05$). Hunted and logged sites had 65% fewer juveniles, with a significant interaction of habitat with distance ($F_{1,38} = 5.35, p < 0.05$): 82% fewer juveniles

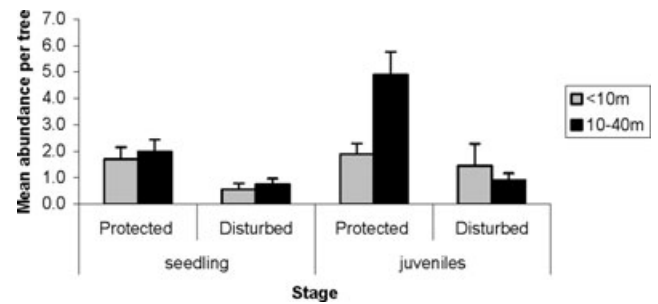


Figure 3. Mean (SE) seedling and juvenile recruits per tree as a function of distance from the tree and protection status of the area for *D. binectariferum* (Meliaceae). Untransformed data are presented. Analyses are from log-transformed data.

regenerated beyond 10 m in disturbed sites compared with protected ones (Fig. 3).

Habitat affected *P. simiarum* seedlings ($F_{1,2} = 129.60, p < 0.01$), but like *D. binectariferum*, there was no interaction of habitat with distance ($F_{1,38} = 0.89, p = 0.351$). Overall, there were 82% more seedlings in protected forests. Distance affected *P. simiarum* significantly ($F_{1,38} = 8.55, p < 0.01$); there were 2.5 times more seedlings regenerating under parental crowns than beyond 10 m. For juveniles, habitat was a significant factor, as was distance from the tree ($F_{1,2} = 183.01, p < 0.01, F_{1,38} = 45.68, p < 0.0001$). Disturbed sites had 75% fewer juveniles. This species also showed a significant habitat by distance interaction for juveniles; 73% fewer juveniles recruited away from the tree in disturbed forests than protected ones ($F_{1,38} = 4.50, p < 0.05$) (Fig. 4).

Interactions of habitat with distance were significant for juveniles but not for seedlings of *P. simiarum* and *D. binectariferum*. Thus, both species recruited poorly as juveniles despite seed dispersal. Seedlings were dispersed away from the parents in disturbed sites and subsequently failed to recruit to juvenile stages.

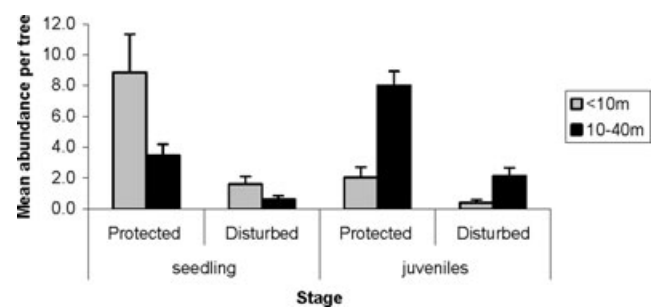


Figure 4. Mean (SE) seedling and juvenile recruits per tree as a function of distance from the tree and protection status of the area for *P. simiarum* (Annonaceae). Untransformed data are presented here. Analyses are from log-transformed data.

Discussion

Reduction of large avian frugivores in overhunted and logged sites potentially disrupts pivotal plant–animal interactions that shape forest communities. Consistent with other reports of declines of some hornbill species (e.g., Datta 1998) and with data we collected in 2008 (P.S., unpublished), hunted and logged sites have depleted populations of Great, Wreathed, and Oriental Pied Hornbills. Because large fruit pigeons at our study sites are not especially targeted by hunters, but eat many of the same fruits as hornbills, pigeons represent a vestige of a redundant dispersal assemblage and could eventually result in density compensation where hornbill densities are low. One of our tree species was severely dispersal limited when hornbills were reduced in numbers, whereas 2 other species experienced some reduction in seed dispersal, but mainly experienced recruitment limitation due to other factors in hunted forests.

Diminished seed dispersal may change recruitment patterns of seedling and juveniles, ultimately reshaping forest communities. In otherwise undisturbed Amazonian forests few recruits near fruiting trees in forest in which primates are commercially hunted suggest inadequate dispersal (Nunez-Iturri & Howe 2007). In the Brazilian Atlantic Forest as many as 33.9% of tree species may be recruitment limited due to loss of seed dispersers (Silva & Tabarelli 2000). In our study area recruitment of large-seeded trees was low at hunted sites with poor juvenile survival at distances > 10 m from parent trees. Our comparison of seedling and juvenile abundances allowed us to distinguish between dispersal limitation and recruitment limitation resulting from other factors.

As predicted, *C. paniculatus*, depended on hornbills for dispersal. Preliminary evidence from protected sites in Pakke indicates high levels of rodent predation (72%) on the seeds (Datta 2001); dispersal away from dense aggregations of seeds and seedlings is probably critical to seed survival and successful seedling recruitment. *C. paniculatus* seedlings failed to disperse beyond areas of high mortality near adult fruiting trees where assemblages of dispersers were depauperate.

We expected *D. binectariferum* to be dispersal limited, perhaps even more so than *C. paniculatus*, given its greater contribution to the diet of hornbills and sparser distribution in the forest. However, seedlings of both *D. binectariferum* and *P. simiarum* were equally abundant near and far from parent trees in disturbed and undisturbed sites; neither showed evidence of poor dispersal. Evidently, alternative dispersers provide adequate dispersal in hunted sites, possibly removing more seeds than they do in intact forests. Focal tree watches in undisturbed forest indicate Imperial Pigeons are important dispersers of *D. binectariferum*, removing 34% of its seeds, but are probably not that important for *C. paniculatus*. No pigeons removed *C. paniculatus* seeds during focal

watches conducted in 2005 and 2006, whereas only 2 seeds were removed at both disturbed and undisturbed sites in 2008 (P.S., unpublished data.).

Large fruit pigeons may act as substitute dispersers in disturbed areas, removing more seeds of *D. binectariferum* and *P. simiarum* in these areas than in protected ones. Great Hornbills sometimes drive away rival foragers (e.g., Wreathed Hornbills). In their absence the Mountain Imperial Pigeon may visit fruiting trees more frequently and remove more seeds. This cannot be assumed because dietary overlaps do not necessarily indicate pigeons are equally effective as seed propagators (Schupp 1993; Howe & Miriti 2004). A 'redundant' frugivore may remove a sufficient number of seeds, but might not compensate for the loss of long-distance dispersal events that hornbills provide, thereby altering patterns of seed dispersal and gene flow (e.g., Jordano et al. 2007).

We do not think this caveat applies to *Ducula* pigeons that, like hornbills, regularly fly long distances (Holbrook et al. 2002; Price 2006). *Ducula* pigeons are extremely important seed dispersers for a variety of tree species in forests of the Asian, Australasian, and Pacific regions (Leighton & Leighton 1983; Corlett 1998; Ganesh & Davidar 2001). They regurgitate and defecate seeds intact and swallow seeds twice the width of their normal gape (Meehan et al. 2002). Additionally, they are highly mobile, dispersing seeds over long distances. For *Ducula pacifica*, estimates of median dispersal distances are 40 km for defecated seeds and 7.5 km for regurgitated seeds (McConkey et al. 2004). This is comparable to 2 species of hornbills, which have been estimated to disperse large seeds up to 3.5 km and 6.9 km in a West African forest (Holbrook & Smith 2000). Hornbills breed when our focal trees are in fruit, so their ranges are reduced (Poonswad & Tsuji 1994) and seed-dispersal distances may be lower. Many seeds may end up in or under breeding cavities with meager prospects for survival. Hornbills and *Ducula* pigeons could be roughly equivalent dispersers, especially during the breeding season.

All our focal trees recruited to the juvenile stage poorly in disturbed areas. Recruitment limitation, in the absence of dispersal limitation, may be due to abiotic or biotic effects in disturbed sites. Hunting and other factors, such as forest fragmentation, may also affect seed and seedling predators (Roldan & Simonetti 2001; Wright 2003; Galetti et al. 2006). In Central America hunting often removes large rodent seed predators and dispersal agents, which favors seedling recruitment even in the absence of effective seed dispersal where rodents are important agents of mortality (Beckman & Muller-Landau 2007; Dirzo et al. 2007; Wright et al. 2007). Poor recruitment of large seeds is likely where seed predators are not hunted, as in forests of western Amazonia, (Nunez-Iturri et al. 2008). At our study sites most rodents were small-bodied and not preferred game. Low recruitment of *D. binectariferum* could occur because of a higher influx of rodents into

disturbed sites or more efficient foraging due to high encounter rates of aggregated seeds or seedlings or could be due to other factors. In any event, recruitment of both *D. binectariferum* and *P. simiarum* was low in disturbed sites even in the absence of dispersal limitation.

The effects of birds on tree recruitment may vary in space and time. Such differences may obscure variations between protected and hunted sites. A low fruiting year in the hunted site, for instance, could result in lower hornbill abundances independent of logging and hunting. Sampling over several years might reveal inconsistent patterns that suggest poor recruitment of trees in disturbed sites is a result of variations in disperser abundance or removal patterns, not hunting or logging. Future studies conducted over multiple years would unequivocally elucidate how bird and tree populations respond to persistent pressures of hunting and logging and whether the patterns we found remain consistent with time. Despite these limitations, our results are highly suggestive of what may happen if hornbills or other such primary dispersers are limited in abundance, irrespective of the cause. The long persistence of tropical forest juvenile trees, in particular, gives the results more power than a single year of bird censuses might imply.

Our results add to the understanding of dispersal limitation and ecological redundancy in defaunated tropical habitats. We are the first to compare the recruitment of multiple large-seeded tree species of low- and high-fecundity that depend on the same limited set of dispersers. Our study builds on work describing dispersal limitation in particular focal species (e.g., Cordeiro & Howe 2003). Uniquely, however, our comparative approach highlights differences in effects of disturbance that studies of individual species might miss. Subtle variations in tree fecundity or size and redundancy of disperser assemblages could cushion mutualisms in otherwise vulnerable large-seeded trees. Our results are consistent with the idea that even among morphologically similar large-seeded trees, those with more functionally equivalent species of frugivores are likely to suffer fewer consequences of extirpation of particular dispersers. Moreover, recruitment collapses in defaunated areas often result for reasons other than disperser loss; distinguishing dispersal from recruitment limitation is important in teasing out the relative importance of each. Our multiple-species approach distinctively does just this.

Destruction of tropical forests eliminates seed dispersers, some of which play pivotal roles in disperser-tree mutualisms (Cordeiro & Howe 2003). Evaluating the ecological specificity and redundancy of disperser roles is critical to maintaining well-functioning tropical forests because it can lead to the design of conservation interventions that forestall or mitigate profound changes in forest composition and structure. In this study, the first to evaluate hunting and logging effects for plant-animal interactions in South Asia, our results suggest that

disturbance alters mutualisms between hornbills and some of their large-seeded food plants, but that multiple outcomes are possible. Loss of dispersers like hornbills could have catastrophic consequences for some trees and their interdependent plants and animals, triggering a spate of extinctions. Role redundancy, however, within even small, specialized disperser assemblages may render others more resistant to loss of regular dispersal agents.

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Supporting Information

Supplementary information on study area, hornbill phenology, frugivores, mega-herbivores and their hunting status (Appendix S1) are available as part of the online article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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