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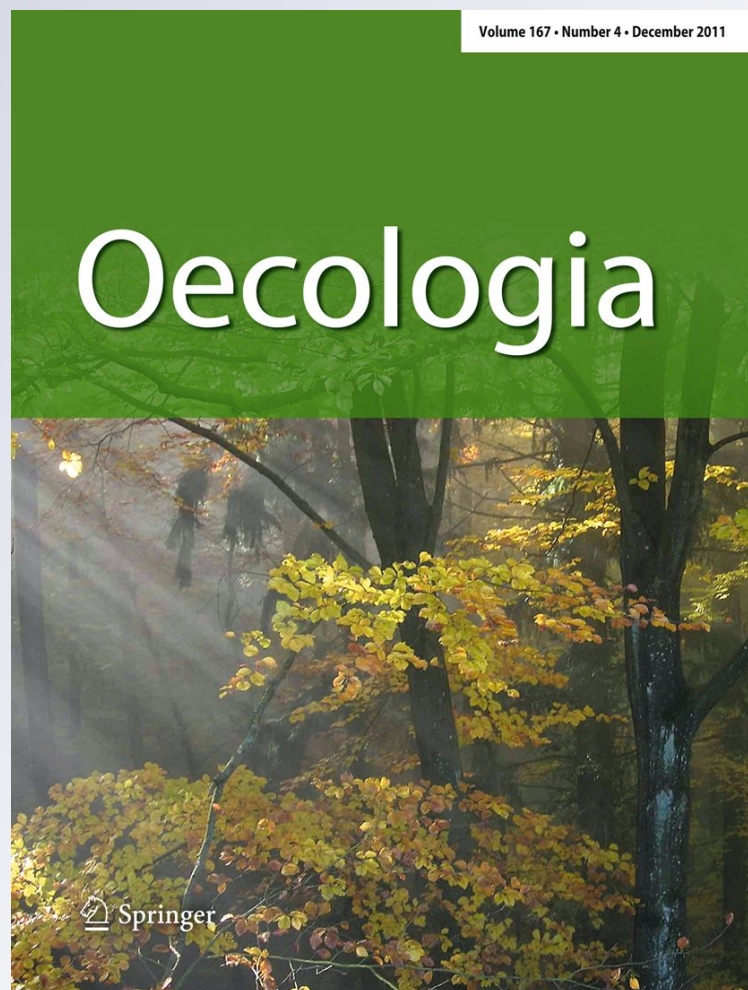
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Oecologia

ISSN 0029-8549

Oecologia

DOI 10.1007/s00442-012-2252-9



 Springer

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Rodent seed predation: effects on seed survival, recruitment, abundance, and dispersion of bird-dispersed tropical trees

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Received: 24 April 2011 / Accepted: 9 January 2012
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Abstract Tropical tree species vary widely in their pattern of spatial dispersion. We focus on how seed predation may modify seed deposition patterns and affect the abundance and dispersion of adult trees in a tropical forest in India. Using plots across a range of seed densities, we examined whether seed predation levels by terrestrial rodents varied across six large-seeded, bird-dispersed tree species. Since inter-specific variation in density-dependent seed mortality may have downstream effects on recruitment and adult tree stages, we determined recruitment patterns close to and away from parent trees, along with adult tree abundance and dispersion patterns. Four species (*Canarium resiniferum*, *Dysoxylum binectariferum*, *Horsfieldia kingii*, and *Prunus ceylanica*) showed high predation

levels (78.5–98.7%) and increased mortality with increasing seed density, while two species, *Chisocheton cumingianus* and *Polyalthia simiarum*, showed significantly lower seed predation levels and weak density-dependent mortality. The latter two species also had the highest recruitment near parent trees, with most abundant and aggregated adults. The four species that had high seed mortality had low recruitment under parent trees, were rare, and had more spaced adult tree dispersion. Biotic dispersal may be vital for species that suffer density-dependent mortality factors under parent trees. In tropical forests where large vertebrate seed dispersers but not seed predators are hunted, differences in seed vulnerability to rodent seed predation and density-dependent mortality can affect forest structure and composition.

Communicated by Walt Carson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2252-9) contains supplementary material, which is available to authorized users.

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Keywords Density dependence · North-east India · Rodents · Seed predation · Seed dispersal

Introduction

Most tropical tree species have aggregated patterns of dispersion but vary widely in their degree of aggregation (Hubbell 1979; Condit et al. 1992; Lieberman and Lieberman 1994). Several factors have been proposed to explain this variation in spatial dispersion. These include post-dispersal events such as seed predation (Janzen 1971), variable seed deposition patterns by primary dispersers (Howe 1989), differences in intra- and inter-specific competitive ability during recruitment (Uriarte et al. 2004), and dispersal modes of tree species (Seidler and Plotkin 2006).

Seed predation by rodents is one of the most important factors affecting seed survival and can exert a strong selection pressure in shaping recruitment and tree

population dynamics (Maron and Simms 1997; García et al. 2005; Siepielski and Benkman 2008). The original template of clumped seeds around parent trees could be altered by seed predators and could have downstream effects on the later life stages of plants (Crawley 1992). Seed predators can cause high overall seed mortality (e.g., sometimes 80% of all seeds produced are preyed upon; Stiles 1989), and correspondingly this results in reduced recruitment, particularly of preferred species. Deposition of seeds in high-density clumps is often associated with increased levels of predation resulting in negative density-dependent survival (Janzen 1971).

Biotic models (incorporating density- and distance-dependent seed predation) predict that the probability of seed survival increases with increasing distance from the parent tree (Janzen 1970; Connell 1971). As a result, a significant decrease is expected in the number of recruits near parent trees (Edwards and Crawley 1999; Howe and Brown 2000). This strong demographic effect is expected to result in more regular spacing and lower abundances of conspecific trees near parent trees than expected from the pattern of seed fall (Janzen–Connell hypothesis). There is substantial evidence for such density- and distance-dependent effects on plant life stages (Connell 1971; Augspurger 1984; Clark and Clark 1984; Harms et al. 2000), an interesting consequence of which is an increase in species diversity in Neotropical forests (Harms et al. 2000; Paine and Beck 2007). Recruitment near parent trees has been shown to vary across species (Chapman and Chapman 1995): common species recruit closer to parent trees, while rare species do not recruit near adults (Terborgh et al. 2002). While some studies have shown that rare species tend to be more aggregated (Hubbell 1979), others have found that most rare species are generally less aggregated (Lieberman and Lieberman 1994). This variation coupled with observations of selective and differential rodent seed predation levels (Kollmann et al. 1998; Rey et al. 2002; Velho et al. 2009) suggests that there may be differences in the degree to which tree species experience density- and distance-dependent mortality at the seed and seedling stages, which can result in differences in adult tree abundance and dispersion patterns.

Most studies investigating relationships between processes acting on different plant life stages have focused on the spatial match between seed deposition by primary dispersers and adult tree dispersion patterns (e.g., Tutin et al. 1991; Fragoso 1997), while other studies have examined the consequences of aggregated seed dispersal on seed and seedling survival and recruitment (Russo and Augspurger 2004; Russo 2005). Often, seeds that are clump-dispersed are the result of dispersal by primates or large herbivores (Tutin et al. 1991; Fragoso 1997; Russo and Augspurger 2004). Seedling and sapling densities were

higher at these clumped seed deposition sites, despite the low per capita seed survival when compared to other parts of the forest (Fragoso 1997; Russo and Augspurger 2004). However, scattered seed deposition has also been shown to be beneficial for seedling recruitment (Wenny and Levey 1998). The pattern of seed deposition by primary dispersers has been suggested to be a plausible mechanism to explain the dispersion and abundance of adult trees (Howe 1989). One of the principal adaptive mechanisms proposed is that species whose seeds are regularly deposited in clumps are likely to have evolved defences against density-dependent mortality in contrast to species that are regularly scatter-dispersed (Howe 1989). Species that are not strongly affected by density-dependent mortality factors at the seed stage (including predation—through proximate factors such as hard endocarps, secondary metabolites, and faster germination; Stiles 1989; Zhang and Zhang 2008) are expected to be able to recruit even at high seed densities below parent crowns, be more common, and have a highly clumped dispersion pattern. Species that have not evolved resistance to density-dependent mortality factors at the seed stage would recruit poorly under parent crowns, would be rare, and would have a well-spaced adult tree dispersion pattern (Howe 1989).

We explored the relatively poorly known links between seed predation and its downstream effects on the different life stages of plants. Specifically, we examined whether patterns in seed survival, recruitment, and adult tree abundance and dispersion are associated. We selected a tropical forest site where tree species vary greatly in adult tree dispersion and density (Datta and Rawat 2008), and rodent seed predation affected seed fates of several tree species (Datta 2001; Velho et al. 2009). We investigated whether density-dependent mortality, particularly seed predation, could explain variation in adult abundance and dispersion patterns (irrespective of causal factors invoked by Howe 1989 for such a response). At this site, we assessed: (1) variation in rodent-mediated seed mortality among six bird-dispersed species and the effect of seed density on such seed mortality, (2) differences in recruitment near and far from parent trees in relation to variation in rodent seed predation, and (3) differences in adult tree abundance and dispersion corresponding to the variation in seed predation and seedling recruitment. We predict that species with relatively low mortality at the seed stage should show relatively high recruitment near parent fruiting trees, be relatively more common, and occur in clumps as adults. Species that suffer high seed mortality should have poor recruitment near parent trees, be less common, and occur widely dispersed as adults. We discuss the consequences of our findings for the long-term structure and composition of tropical tree communities.

Materials and methods

Study area and study species

The study was carried out from December 2007 to May 2008 in the tropical foothill forests of western Arunachal Pradesh, India, in Pakke Wildlife Sanctuary and Tiger Reserve (26°54'–27°16'N, 92°36'–93°09'E, 862 km²). The main vegetation type is classified as Assam valley tropical semi-evergreen forest (Champion and Seth 1968). The dominant tree families are Euphorbiaceae, Lauraceae, and Meliaceae (Datta and Goyal 2008). Several canopy deciduous species dominate the forest in the intensive study site with leaf fall in March–April, while the sub-canopy and understory is dominated by evergreen species. Some of the common tree species are *Polyalthia simiarum*, *Pterospermum acerifolium*, *Sterculia alata*, *Stereospermum chelonoides*, *Ailanthus grandis*, and *Duabanga grandiflora*. A high percentage of tree species (64%) are animal-dispersed, with 12% of tree species being wind-dispersed (Datta and Rawat 2008). The intensive study site was located in the south-eastern periphery of the reserve and has had a past history of disturbance with some selective felling of tree species having occurred 35–40 years ago, prior to declaration of the area as a sanctuary in 1977. The important avian frugivores in the area are three species of hornbills: *Buceros bicornis* Linnaeus (Great Hornbill), *Rhyticeros undulatus* Shaw (Wreathed Hornbill) and *Anthracoceros albirostris* Shaw and Nodder (Oriental Pied Hornbill). There are between 45 and 50 other frugivorous bird species in the area (Datta and Rawat 2008).

The pre-dispersal seed predators found in the study area include four species of diurnal tree squirrels (Datta and Goyal 2008). Among the terrestrial rodent species known to occur in the area, *Hystrix brachyura* Linnaeus (Himalayan crestless porcupine), *Atherurus macrourus* Linnaeus (Brush-tailed Porcupine), *Niviventer* sp., *Rattus* sp., and *Berylmus* sp. were the main post-dispersal seed predators. Scatter-hoarding levels were low with only 1.43% of 1,390 tagged seeds cached (Velho et al. 2009).

We selected six medium- to large-seeded (>2 cm) tree species with lipid-rich fruits that are among the most important species in the diet of hornbills (Datta 2001). Ripe fruits of *Prunus ceylanica* Miq. (Rosaceae) and *Canarium resiniferum* Brace (Burseraceae) were available from December to January. Fruiting of *Dysoxylum binectariferum* Roxb., *Chisocheton cumingianus* Buch.-Ham. (both Meliaceae) and *Horsfieldia kingii* Hook. (Myristicaceae) occurred from February to May. The main fruiting period of *Polyalthia simiarum* King (Annonaceae) is from May to July, while a minor fruiting peak also occurred from December to February (Datta 2001; Velho et al. 2009).

Sampling design

Effects of varying initial density on seed removal and mortality for six tree species

To assess mortality risk faced by seeds deposited in varying densities, 15 plots (1 × 1 m) were set up with varying seed densities for each of the six study species (median_{all plots × all species} = 55; range = 1–108 seeds). Previous work at this site (Datta 2001) reported that hornbills (a primary disperser of these species) deposit seeds at densities of 100 (±SD 32.73) m⁻² at nest trees, 44 seeds (±SD 34.76) m⁻² at roost trees, and 1 (±SD 0.16) m⁻² at perch trees. Therefore, to adequately represent the range of seed densities resulting from biotic dispersal, for each species, we chose 15 seed densities randomly from a uniform distribution ranging from 1 to 108 seeds m⁻². For all six species, intact seeds were collected from ripe fruits under parent fruiting trees and set out in the plots.

Successive plots were separated by 50 m to maximize independence between them. The number of seeds removed were monitored every alternate day. Seeds removed from plots were assumed to have been preyed upon by rodents, as a study that was carried out over the same period and in the same intensive study area found almost no scatter-hoarding (Velho et al. 2009). Seed mortality due to others factors, such as infestation by insects was recorded separately. We monitored seeds until establishment, which was defined as the emergence of the cotyledons.

Recruitment near and far from parent fruiting trees

We selected 6–10 fruiting individuals of each of five of the six tree species to quantify recruitment patterns near and far from parent fruiting crowns. For *P. simiarum*, we sampled 20 trees. At the base of each fruiting tree, we established a wedge-shaped plot that was randomly directed with its apex at the tree base. The angle of the apex was 20° and the two limbs of the plot radiated up to 30 m from the tree base for all plots of all species (Cordeiro and Howe 2003). Starting from the base of the parent tree, we counted all recruits up to 100 cm in height in 2-m distance intervals up to 30 m within the wedge-shaped plot. We selected individual trees that were located away from other conspecific adult trees in the forest. We enumerated all recruits at the end of the fruiting period for each individual tree.

Adult tree species density and dispersion

We established 22 (50 × 50 m) plots at randomly selected locations in a 10-km² intensive study area (which has an

undulating terrain and semi-evergreen forest), to determine adult tree abundance and dispersion patterns. We followed Clark and Evans (1954) to compute an index of spatial dispersion based on densities and the nearest neighbor distances of adult trees. Therefore, we chose to have a number of smaller plots across the study area (as opposed to a single plot of a larger size), as rare tree species such as *P. ceylanica* and *H. kingii* were likely to be under-represented in a single plot.

In each plot, the number of adult trees of the six species were enumerated. Adult trees were defined as those with girth at breast height (GBH) ≥ 30 cm. We measured the nearest neighbor distances of each tree to a conspecific within the plot. If the nearest conspecific was outside a plot, the nearest neighbor distance was still measured. For rare, widely spaced species, such as *H. kingii* and *P. ceylanica*, it was difficult to manually measure distances to conspecifics located far outside the plot. For these two species, co-ordinates of each tree in the intensive study site were recorded using a GPS unit (Garmin GPS 12XL; UTM) to calculate nearest neighbor distance. In total, we obtained nearest neighbor distances of 27 individuals of *H. kingii*, 18 individuals of *P. ceylanica*, 34 individuals of *C. resiniferum*, 30 individuals of *D. binectariferum*, 93 individuals of *P. simiarum*, and 98 individuals of *C. cumingianus*.

Statistical analyses

Density dependence and overall mortality of seeds

All analyses were carried out using the statistical software R (v.2.8.0) (R Development Core Team 2009). We used survival analyses, specifically Cox proportional hazards models (Therneau and Grambsch 2000) to examine variation in overall and density-dependent seed mortality across species.

Polyalthia simiarum seeds had a beetle larvae infestation which resulted in rotting of seeds. We therefore censored all rotten seeds of this species during survival analysis on the day that rotting was noted. A Cox-proportional hazards model with mixed effects was used to model the effect of species and initial seed density on seed survival (Therneau and Grambsch 2000; coxme package in R, Therneau 2009). As seeds within a plot are unlikely to be independent samples, plot identity was included as a random effect. An interaction between initial seed density and species was also included in the statistical model. Likelihood ratio tests were used to examine the significance of both fixed and random effects. Model criticism was performed in two ways. The mixed effects from the model were extracted and added as offsets to a fixed effects Cox model and then the key assumption of proportional hazards

was evaluated (T.M. Therneau, personal communication). In addition, we fitted a fixed effects Cox proportional hazards model with all the predictors included in the mixed effects model but without plot identity as a random effect, and evaluated assumptions of proportional hazards, linearity of the predictor, and influence of individual data points.

Recruitment near and far from parent fruiting trees

Data from the wedge-shaped plot were divided into two classes; near (0–10 m from trunk) and far (10–30 m from trunk). A generalized linear mixed effects model (GLMM) with Poisson errors and a log link was used to model the effect of species and distance from the parent tree on the number of recruits. Near and far plots of a given tree may show non-independence, therefore we included tree identity as a random effect. The number of recruits was the response variable, and species and distance-class (and the interaction) were predictor variables. Area was included as an offset in the GLMM to take the unequal area into account (our wedge-shaped sampling method produced a larger sampling area further from the tree).

To examine the relationship between seed predation and recruitment across tree species, we ran a Spearman's rank correlation between estimated seed mortality and mean recruits m^{-2} near the parent trees. As sample size was limiting ($n = 6$ species), we used a randomization test with 10,000 iterations to assess significance. To allow for density-dependent changes in seed mortality within a species (rather than using a single estimate of seed mortality for a species), we used seed mortality estimates from the survival analyses calculated at two initial seed densities, namely low ($10 m^{-2}$), and high ($60 m^{-2}$), and ran separate correlations between seed mortality at each of these seed densities and mean recruits m^{-2} near the parent trees. These density values represent the midpoints of low and high density classes and were used later to visualise seed survival across species (see "Results"). These density categories were chosen based on seed densities seen in the area.

Adult tree species dispersion

The latitude–longitude co-ordinates of individual trees were downloaded and projected to the Universal Transverse Mercator (UTM) 46 N (WGS-84 datum). The nearest neighbor distances were calculated using the package Spatstats (Baddeley and Turner 2005) in R. These distances were then used to calculate the Clark and Evans's index (1954) which expresses the degree to which the observed distribution of nearest neighbor distances deviates from

that expected if the population were distributed at random (while accounting for density). The index of clumping ranges from 0 (most clumped) to 2.15 (most scattered).

The measure of spacing from Clark and Evans (1954) is computed as:

$$\bar{r}_a = \frac{\sum r}{N}$$

where r = the distance in any specified units from a given individual to its nearest neighbor, N = the number of measurements of distance taken in the observed population or sample, \bar{r}_a = the mean of the series of distances to the nearest neighbor, and $\sum r$ = the summations of the measurements of the distance to the nearest neighbor.

$$\bar{r}_e = \frac{1}{2\sqrt{\rho}}$$

ρ = the density of the observed distribution expressed as the number of individuals per unit area

\bar{r}_e = the mean distance to the nearest neighbor expected in an infinitely large random distribution of density ρ

$$R = \frac{\bar{r}_a}{\bar{r}_e}$$

R = the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbor. To test for a relationship between recruitment and adult tree dispersion, we used a Spearman's rank correlation with a randomization test with 10,000 iterations. This tested for correlations between the mean number of recruits under parent trees and the index of spatial dispersion of adult trees.

Results

Effects of varying initial density on seed removal and mortality for six tree species

A total of 2,394 seeds were set out across all six species. Inter-species differences in seed predation levels ranged from 4.1% in *C. cumingianus* to as high as 98.7% of all seeds depredated in *D. binectariferum* (Table 1). Of the six species, seed mortality due to predation was lowest for *P. simiarum* and *C. cumingianus* (27.4 and 4.1%, respectively). The percentage of seeds preyed upon for the other four species was much higher (78.5–98.7%). Removal of seeds from plots for four of the six species began from the fourth to sixth days after the start of a trial; the exceptions, *P. simiarum* and *C. cumingianus*, had little or no removal. In general, for the four species with substantial seed removal, the trend at higher seed densities was that of rapid

removal during the 1 month. At lower seed densities, there was more variation in seed removal rates with *D. binectariferum* showing the greatest removal rate; most seeds of this species were preyed upon immediately (only 21 out of 399 were left by day 20).

These differences among species in (1) overall susceptibility to removal by predators, and (2) density-dependent seed removal were formally tested using a mixed effects Cox proportional hazards model. The monitoring time ranged from a minimum of 56 days for *C. cumingianus* to a maximum of 148 days for *P. ceylanica*. In our analysis of seed removal under varying initial density and across species, we censored observations at 30 days as seeds might start to become unattractive to rodents thereafter (we also obtained a similar result when we censored observations at 60 days).

The estimated effect of initial seed density and species on hazard ratios (relative risk of mortality) was substantially non-additive (likelihood ratio test; interaction term of density \times species $\chi^2 = 87.74$, $df = 5$, $P < 0.001$), indicating that the strength of density dependence varied across species. *Dysoxylum binectariferum*, *H. kingii*, *P. ceylanica*, and *C. resiniferum* showed relatively high overall mortality and a sharp increase in mortality with density. By contrast, *P. simiarum* and *C. cumingianus* showed low overall mortality and a weak increase or a decrease in mortality with density (Fig. 1).

To visualize changes in survival with seed density, we plotted survivorship curves for each species at low and high seed densities. This was done by categorizing plots with 1–20 seeds m^{-2} (mean = 10 seeds m^{-2}) as low seed density plots and plots with more than 20 seeds m^{-2} (mean = 60 seeds m^{-2}) as high seed density plots. For each species, we estimated survivorship curves using the Kaplan–Meier estimator pooling together seeds from plots in each density class. Consistent with the estimated relationships from the mixed effects model, at low densities, *D. binectariferum*, *H. kingii*, and *P. ceylanica* showed the greatest decrease in survival over time (Fig. 2a), although at low seed densities, *C. resiniferum* showed little change in survival over time. At high densities (>21 seeds), these three species and *C. resiniferum* showed even more rapid declines in survival, indicating negative density-dependent survival (Fig. 2b). *Polyalthia simiarum* and *C. cumingianus* showed relatively low declines in survival at both low and high densities.

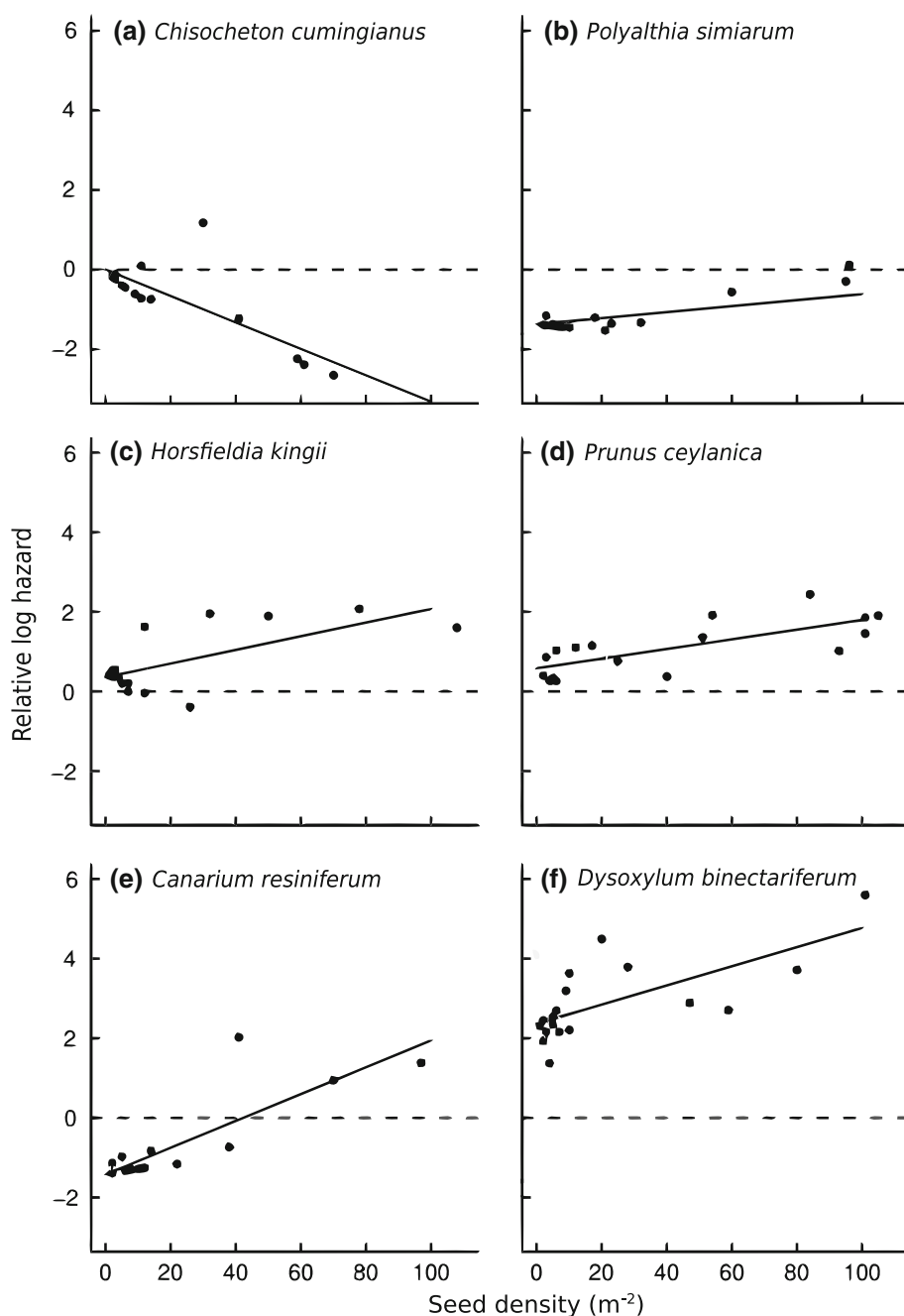
Polyalthia simiarum had high infestation by insects at most sites after 20 days. However, despite the mortality due to infestation, *P. simiarum* showed lower overall seed mortality (54.1%) compared to the other species. Furthermore, seed predation by rodents alone accounted for only 27.4% of seed mortality in this species. In contrast, for all other species except *C. cumingianus*, seed predation by

Table 1 The percentage of seeds removed/preyed upon by rodents for the six tree species arranged in order of increasing predation levels

Species	Total seeds	Preyed upon (%)	Rotten (%)
<i>Chisocheton cumingianus</i>	297	4.1	0
<i>Polyalthia simiarum</i>	390	27.4	26.67
<i>Horsfieldia kingii</i>	349	78.5	0
<i>Canarium resiniferum</i>	351	80.62	0
<i>Prunus ceylanica</i>	608	92.1	0
<i>Dysoxylum binectariferum</i>	399	98.74	0

Only seeds of *Polyalthia simiarum* were recorded to be rotting

Fig. 1 Results from the mixed effects Cox proportional hazards model showing model estimates for how relative risk of seed mortality (relative log hazard) varied across species and density. The estimated relative log hazard represents the multiplicative change in risk due to changes in density and species. The mixed effects model takes into account the non-independence of seeds within 1×1 m seed plots. For each species, *lines* represent estimated fixed effects (change in relative risk with changing density) while *each point* represents the estimated fixed and random effects for a given plot. Random effects represent the estimated departure of relative risk of seed mortality for individual plots from the estimated average effect arising from plot-specific differences in unmeasured variables (block effects)



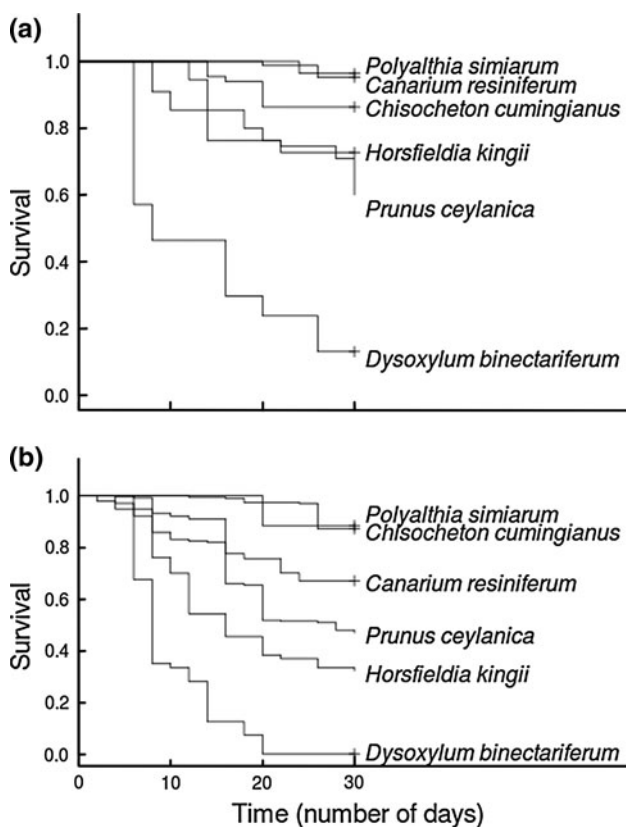


Fig. 2 Kaplan–Meier survivorship curves for each species: **a** at low (<21 seeds m^{-2}) and **b** high (>21 seeds m^{-2}) seed density classes. Observations were censored at 30 days

rodents ranged from 78.5 to 98.7% (Table 1). *Polyalthia simiarum* was the only species in which infestation by insects was noted. Retaining the seeds that were infested (without censoring) in a survival analysis produced similar results.

Recruitment near and far from parent fruiting trees

Seedling and sapling recruitment varied with distance from the parent tree, and the difference in the number of recruits between near (within 10 m from the base of the trunk) and far (10–30 m from the base of the trunk) distance classes varied across species (GLMM with Poisson errors; likelihood ratio test for the interaction term distance \times species $\chi^2 = 15.62$, $df = 5$, $P < 0.01$).

Polyalthia simiarum and *C. cumingianus* showed the highest recruitment (mean = 6.05 and 1.3 recruits m^{-2}) near the parent tree, *C. resiniferum* and *D. binectariferum* had lower recruitment (mean = 0.6 and 0.2 recruits m^{-2}), while *H. kingii* and *P. ceylanica* showed no recruitment near parent trees (Fig. 3). In general, average recruitment far from parent trees ranged from 0 to 0.5 recruits m^{-2} . Using correlations with a randomization test, we tested the relationship between overall mean mortality at low

(10 m^{-2}) and high (60 m^{-2}) seed densities and the mean recruits m^{-2} near the parent trees. The relationship was tested at a relaxed α level of 0.1 because of the low statistical power and sample size (six tree species). We found a negative relationship between overall mean mortality at low (10 m^{-2}) and high (60 m^{-2}) seed densities, and the mean number of recruits under parent trees (Spearman rank correlation and one-tailed P value; low: $r_s = -0.75$, $p = 0.08$; high: $r_s = -0.75$, $P = 0.08$).

Adult tree species abundance and dispersion

Tree species varied widely in the dispersion of adults. Some species (*C. cumingianus* and *P. simiarum*) had conspecifics within 10 m from each other, while individuals of *H. kingii* were separated by distances greater than 100 m. Based on the Clark and Evans's index of dispersion, *P. simiarum* was the most aggregated, while *H. kingii* had maximum spacing between individuals (Table 2). The two most aggregated species (*P. simiarum* and *C. cumingianus*) were the most common species, whereas the two rarer species (*H. kingii* and *P. ceylanica*) were also more widely spaced (Table 2).

We also found that the species that had lower seed predation levels (*C. cumingianus* and *P. simiarum*) were more clumped and abundant in the habitat compared with species that suffered from higher predation (*C. resiniferum*, *D. binectariferum*, *H. kingii*, and *P. ceylanica*). The correlation analysis with randomization tests showed a negative relationship between mean number of recruits under parent crowns and the index of dispersion (Spearman's $r_s = -0.92$, one-tailed $P = 0.007$), which indicates a positive relationship between the number of recruits and the increasing aggregation of adult trees.

Discussion

Our study provides insights towards a mechanistic understanding of the biotic factors underlying the abundance and dispersion of tropical forest trees. We present evidence to support the idea that variation in adult tree abundance and dispersion patterns can result from variable levels of species-specific and density-dependent predation at the seed stage. Seed predation varied widely across the six study tree species. Density effects on seed survival were also variable, with species that suffered high overall mortality showing stronger negative density-dependent survival. A similar variation in the relationship between seed density and survival has been found in other studies (Hulme 1994; Romo et al. 2004).

If seed predation is an important factor influencing recruitment around parent trees, variation in seed predation levels should correlate with variation in recruitment around

Fig. 3 Mean density of recruits (per hectare) near and far from parent trees for each species. The number of sampled trees is denoted by n for each species. Error bars indicate standard errors of the mean density of recruits per hectare

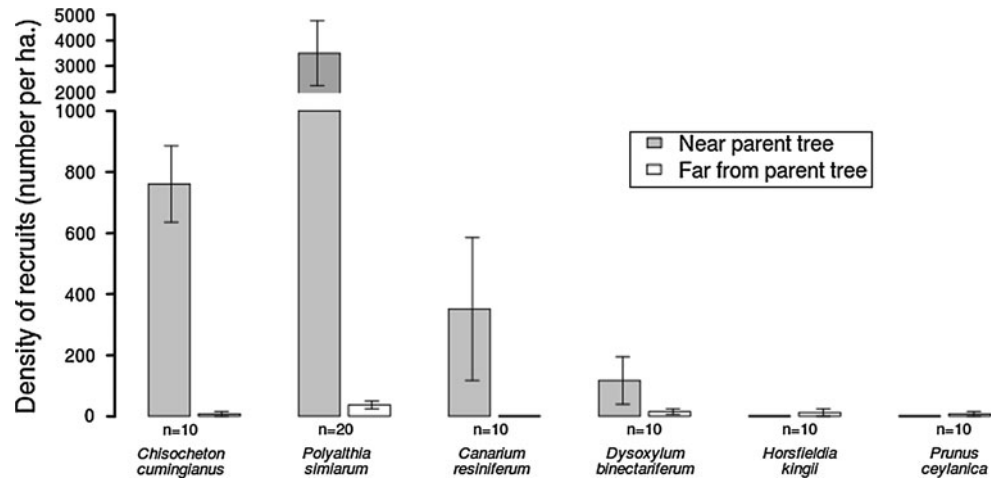


Table 2 The index of dispersion for adult trees arranged in increasing order of scatter, where the value of R ranges from 0 (maximum clumping) to 2.15 (maximum spacing of individuals)

Species	Seeds preyed upon (%)	Mean NND (m)	No of trees ha^{-1}	SE tree density	Index of dispersion (R)	SE (R)
<i>Polyalthia simiarum</i>	27.4	4.50	16.90	0.43	0.37	0.03
<i>Chisocheton cumingianus</i>	4.1	6.18	17.82	0.29	0.52	0.04
<i>Dysoxylum binectariferum</i>	98.74	15.31	4.36	4.42	0.64	0.05
<i>Canarium resiniferum</i>	80.62	15.00	6.18	3.14	0.75	0.06
<i>Prunus ceylanica</i>	92.1	63.07	0.73	1.20	1.08	0.26
<i>Horsfieldia kingii</i>	78.5	131.35	0.54	1.22	1.94	0.34

Tree density computed per hectare

NND nearest neighbor distance

parent trees. Consistent with this idea, we found that *C. cumingianus* and *P. simiarum* had a substantially smaller proportion of seeds preyed upon and higher recruitment near parent fruiting trees compared to the other four species (Table 1; Fig. 3). Furthermore, these differences between species in recruitment were correlated with adult tree dispersion patterns, suggesting that processes acting at the seed stage can have important downstream effects. Our work shows that species differ in overall, as well as density-dependent mortality at the seed stage. Species that are subject to low levels of rodent seed predation at the seed stage are more common and have a highly clumped dispersion pattern when compared with species that may have not evolved defenses to resist such mortality factors. We found that one of the species (*P. simiarum*) experienced insect attack at high densities—another possible density-dependent mortality factor that could have downstream effects on adult tree dispersion patterns.

Seed predation can play a key role in influencing plant population dynamics if seed mortality results in fewer recruits (Maron and Simms 1997). When seed predation has variable effects on different species, it also has the potential to drive relative abundance patterns of species. Both pre- and post-dispersal seed predators (insects or

rodents) are important biotic agents influencing plant recruitment (Louda 1982; García et al. 2005; Orrock et al. 2006; Paine and Beck 2007; Siepielski and Benkman 2008; Bricker et al. 2010). However, most evidence for the effects of seed predation on plant recruitment has been from arid communities (Brown and Heske 1990), mesic grasslands (Edwards and Crawley 1999), perennial herbs and forbs (Orrock et al. 2006; Bricker et al. 2010). Evidence linking post-dispersal seed predation in structuring adult tree distribution patterns is sparse for woody plant species (see Schupp 1992), although there are studies linking rodent seed predation and recruitment in both temperate and tropical forests (e.g., Schupp 1990; Wenny 2000; García et al. 2005).

While the number of species we focused on was constrained to be low as a result of the detailed information needed on different life stages, our findings clearly indicate that species with the lowest seed predation levels showed more recruitment under parent fruiting trees and the highest amount of adult tree aggregation. It is generally accepted that the seed to seedling transition is the most critical stage in determining plant recruitment in larger size classes (Harms et al. 2000; Wright et al. 2005). In this study, we did not directly examine the role of other demographic

filters, such as insect and mammal herbivores (Connell 1971) and plant pathogens (Augspurger 1984; Bell et al. 2006) that can play an important role after seedling emergence in determining spatial patterns of recruitment. In addition, we did not determine the abundance and distribution patterns between the sapling and adult stage. Several other mortality risks and demographic filters (light availability and intraspecific competition) are likely to operate at this stage. For tropical trees, factors affecting the juvenile stage might not be important as the main risk period is during the seed and seedling stage (Harper 1977), and the role of competition in driving these patterns has been considered to be unimportant (Wright 2002; Paine et al. 2008). However, our study does not address whether these factors play an important role in determining life-stages of our study species.

For the six species we studied, we have demonstrated that species-specific variation in rodent predation with variable density-dependent effects at the seed stage appears to have an important effect on adult tree abundance and dispersion. However, the relative effects of inter-specific differences in overall seed mortality versus inter-specific differences in density-dependent seed survival on recruitment and adult tree dispersion, and the direct role of other mortality factors that could reduce or magnify the effect of variable rodent seed predation need to be further investigated. Also, the generality of these patterns needs to be tested for other species.

The main functional consequences of variable seed predation for tropical tree communities are the importance of biotic seed dispersal, and possibly poor regeneration in its absence. For species that exhibit high density-dependent mortality and low recruitment near parent crowns because of high seed predation levels (such as *H. kingii*, *P. ceylanica*, *D. binectariferum*, and *C. resiniferum*), primary dispersers may be vital in aiding escape and colonization to new sites. On the other hand, species such as *C. cumingianus* and *P. simiarum* that are not preyed upon as much and have greater recruitment near parent trees may be able to recruit in the absence of dispersers. Such species are likely to suffer fewer consequences if the abundances of primary dispersers decline (Sethi and Howe 2009). At sites where large vertebrate dispersers disappear due to intensive hunting, seed predators such as rodents may remain unaffected as they are often not specifically targeted by hunters (Wright et al. 2007). This is likely to result in (1) poor dispersal, and (2) greater seed predation rates for tree species that are vulnerable to seed predators. In the long term, the decline of vertebrate dispersers and consequent disruption of such plant–animal interactions are likely to affect plant communities resulting in changes in forest structure and composition.

Acknowledgments This work was funded by the Wildlife Conservation Society–India Program. The Nature Conservation Foundation, Mysore, helped with logistics and equipment. We thank the Arunachal Pradesh Forest Department for granting permission and facilitating the fieldwork. All experiments in this study comply with current Indian laws. Kishore Dorje, Kumar Thappa, Tagge Talang, Rajan Bahadur, Rasham Barra and Narayan Mogar made this work possible with their immense support in the field. Suhel Quader, Jason Tylanakis, Robert Chandran and T.M. Therneau helped with data analyses. Geoff Hyde and Ajith Kumar helped with the structure and content of this manuscript. Umesh Srinivasan helped at all stages of the manuscript, especially ensuring its completion. We thank Eugene Schupp, Maurie Beck and Walter P. Carson for valuable comments that helped improve our manuscript.

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