Experimental Seed Predator Removal Reveals Shifting Importance of Predation and Dispersal Limitation in Early Life History Stages of Tropical Forest Trees

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Abstract Recruitment limitation of trees in tropical forests can occur because of high rates of seed predation or low rates of seed dispersal, but the degree to which limitation is influenced by variation in seed predator abundance, and hence variation in seed predation and dispersal, is not well understood. We experimentally reduced the density of a granivorous small mammal (*Heteromys desmarestianus*) by 90 % to assess the degree to which its rates of seed predation and dispersal limit seed to seedling survival of nine species of trees in a Neotropical lowland forest. Overall, the proportion of seeds that germinated was influenced more by high rates of predation than by limited dispersal. Reduction in density of *H. desmarestianus* resulted in an order of magnitude decrease in fruit removal rates and an order of magnitude increase in both the absolute and relative numbers of seeds that germinated. However, the proportion of seeds that were cached remained relatively constant across all periods and between control grids and removal plots. In removal plots, *H. desmarestianus* dispersed and cached about 10 % of the fruits they handled, of which approximately 25 % germinated. This was 2 to 3 times greater than the germination rates of undispersed seeds, and for two species dispersed seeds were the only ones that germinated. The results suggest the simultaneous occurrence of both seed predation and dispersal limitation for trees with animal-dispersed seeds, but there may also be a hierarchy of importance in the relative strength of these two mechanisms that is determined by the dynamics of seed predator populations.

Keywords Dispersal limitation · Diversity maintenance · Predation limitation · Seed dispersal · Seed limitation · Seed predation · Small mammals · Tropical forests

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Plant nomenclature Balick et al. (2000)

Introduction

Recruitment limitation is currently regarded as one of the key factors that maintain high levels of tree diversity in tropical forests (Hubbell et al. 1999; Harms et al. 2000; Muller-Landau et al. 2002; May et al. 2012). It can occur as a result of two general mechanisms: seed limitation and establishment limitation (Table 1). Seed limitation can occur because of reduced levels of seed production ("source limitation"), seed dispersal ("dispersal limitation"), or post-dispersal survival ("post-dispersal limitation"), while establishment limitation can occur when there is restricted availability of safe sites for seeds to germinate and survive (Muller-Landau et al. 2002; Schupp et al. 2002; Table 1). Seeds of many tree species in tropical forests fail to be dispersed, indicating that seed limitation is quite prevalent (Makana and Thomas 2004; Dalling 2005; Svenning and Wright 2005). Seed limitation for species whose seeds are dispersed by animals can occur when there are high rates of seed predation (predation limitation), low rates of seed dispersal (dispersal limitation), or both (Crawley 2000; Münzbergová and Herben 2005). This suggests that the strength of seed limitation will often be determined by an interaction between seed predation and seed dispersal; if rates of seed predation are high and seed dispersal low then seed limitation would be expected to be strong, but high rates of seed dispersal would weaken its importance (Webb and Peart 2001).

Table 1 An outline of recruitment limitation mechanisms in plants. Note that predation can be a mechanism for both seed and establishment limitation

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1. Seed limitation (flowers ➔ germinating seeds)
    a. Source limitation (flowers ➔ viable seeds)
        i. Abiotic
        ii. Pollination failure
        iii. Pre-dispersal seed predation
    b. Dispersal limitation (viable seeds ➔ final deposition)
        i. Primary
        ii. Secondary
        iii. Tertiary
    c. Post-dispersal limitation (final deposition ➔ germination)
        i. Abiotic
        ii. Seed longevity
        iii. Post-dispersal seed predation
2. Establishment limitation (germinating seeds ➔ juveniles)
    a. Abiotic
    b. Pathogens
    c. Herbivory
    d. Competition

Note: Terminology synthesized from Crawley (2000), Muller-Landau et al. (2002), and Schupp et al. (2002).

Mammals, particularly rodents, ungulates, and marsupials, play important roles as both seed predators and dispersers (Forget and Hammond 2005). Many studies have shown that seed predation and dispersal patterns can be altered as a result of changes in mammal communities (Asquith et al. 1997; Forget et al. 1998; DeMattia et al. 2004), and it is well established that individual mammal species can have a strong influence on rates of seed predation and dispersal (Hoch and Adler 1997; Asquith et al. 1999; Klinger and Rejmánek 2009). Fluctuations in abundance of mammal populations in tropical forests can be large and appear to be tied closely to food resources (Wright et al. 1999; Klinger 2006), and it has been hypothesized that seed predation and dispersal rates will differ during phases of population increase and decrease (Hammond and Brown 1998; Forget et al. 2002). Correlation of these rates to fluctuations with abundance of mammal seed predator populations have been reported (Curran and Webb 2000; DeMattia et al. 2004; Klinger and Rejmánek 2009, 2010), which suggests that the strength of seed limitation could often be an outcome from mammal community and population dynamics. But it also implies that the strength of seed limitation will vary substantially over time and across tree species. If one or a few species dominate a seed predator assemblage then changes in their abundance should be reflected in changes in seed predation and dispersal rates. This, in turn, would be expected to result in increased or decreased rates of seed to seedling survival ("seed germination rates" from hereon). For instance, if a decrease in seed predation by one seed predator species was compensated for by increased predation from another species, then the strength of seed limitation may remain constant, with its strength determined by the proportion of seeds consumed *vs* dispersed. But if the decrease in seed predation was not compensated for then the strength of seed limitation could weaken.

The most direct way to test the strength of seed limitation would be to manipulate seed predator abundance and measure how this altered rates of seed dispersal, seed predation, and germination. To the best of our knowledge though, this approach has not been used in studies of recruitment limitation in tropical forests. Therefore, our goal was to evaluate the degree to which the experimental removal of a small mammal seed predator (spiny pocket mouse, *Heteromys desmarestianus* Gray: Heteromyidae) in a lowland forest of Central America resulted in shifts in rates of predation and dispersal for seeds of different tree species. We knew from previous studies that the forest we were working in had a relatively large community of mammal granivores and frugivores, but abundance of *H. desmarestianus* was 1–2 orders of magnitude greater than that of other small mammals in the forest (Klinger 2006, 2007) and that it was an important seed disperser as well as seed predator (Brewer and Rejmánek 1999; Klinger and Rejmánek 2010). Functional response experiments indicated high rates of seed predation on many tree species (Klinger and Rejmánek 2009), but we could only indirectly relate seed predation and dispersal to variation in abundance of *H. desmarestianus* and were unable to estimate germination rates. In this study we directly compared fruit removal rates, seed fate, and germination for nine tree species before, during, and after a three month period when we reduced the density of *H. desmarestianus* >90 %. The tree species were selected to represent different periods of natural fruiting phenology and we reasoned that the only period we should see markedly different removal and dispersal patterns would be when abundance of *H. desmarestianus* was reduced. Specifically, we hypothesized that: (1) seed predation and dispersal rates would not be compensated for by other small mammals after reduction in density of *H. desmarestianus*; (2) prior to reduction and after

H. desmarestianus population recovery there would be the greatest potential for predation limitation (high rates of fruit removal and seed consumption and low germination rates); (3) in plots where density of *H. desmarestianus* was reduced there would be virtually no seed predation or dispersal, but germination rates would substantially increase; (4) reduction in density of *H. desmarestianus* would lead to a decrease in the absolute number but not the proportion of seeds dispersed; and, (5) the proportion of scatterhoarded seeds that germinated would be similar to that germinating in exclosures.

Methods

Study Area

The study was conducted from January 2004 to March 2005 in a 5 km^2 section of the Bladen Nature Reserve (BNR), Toledo District, Belize (16°33′ N, 88°43′ W). The BNR is located in the southeastern region of the Maya Mountains, 350 km^2 in area, and surrounded by three forest reserves, a national park, and a wildlife reserve. The annual rainfall is typically 2,500–3,000 mm, with 67 %–81 % falling during the wet season (June–January; Belize Foundation for Research and Environmental Education, unpubl. data collected 1997–2005). The temperature is relatively constant throughout the year, with mean annual daily minimum and maximum of 24°C and 30°C, respectively. Vegetation is comprised of evergreen tropical forest (Brewer et al. 2003). The fauna and flora are intact, but abundance of large and medium-sized mammal seed predators is not high (R. Klinger, unpubl. data). Species richness of small mammal granivores and frugivores is high but evenness is quite low, with *H. desmarestianus* being the dominant species across seasons and years (Klinger 2006).

Trapping Protocols

Mark-recapture trapping was conducted in six permanent 0.5 ha plots (grids from hereon) to estimate abundance of *H. desmarestianus*. Distance between the grids ranged from 125–375 m. Three of the grids were randomly selected to be control grids (no removal of *H. desmarestianus*) and three as removal grids (removal of *H. desmarestianus* for three months; DR grids from hereon). Trapping stations in all grids were set in a 10 × 10 array with 7-m spacing between them. A single Sherman live trap (Model XLK; 8 cm × 10 cm × 38cm) baited with a mixture of whole peanuts, raw corn kernels mixed with peanut butter, and a slice of banana or plantain was placed at each station.

Trapping in all six grids was conducted in eight primary periods: January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004, and March 2005; trapping was conducted for five consecutive days within each period (Pollock et al. 1990). Traps were kept open 24 hrs/day and checked each morning.

The density of *H. desmarestianus* was reduced in the three DR grids from 22 May to 12 August 2004. Trapping was done until all *H. desmarestianus* were removed (2–5 days) in each DR grid every other week. Individuals removed from the grids were kept for feeding trials and not returned to the wild (R. Klinger, unpubl. data). Trapping was not conducted in the control grids from May through July because of time constraints associated with the removal trapping. After 12 August density of *H.*

desmarestianus in the DR grids was allowed to re-establish through natural immigration and reproduction.

Fruit Removal and Fate

Two experiments were done to compare removal rates of fruits before, during, and after density reduction of *H. desmarestianus*. The first experiment ("short-term" from hereon; Table 2) was conducted in each of five periods; two prior to density reduction of *H. desmarestianus* (February and May 2004), one during the period of density reduction (June 2004; removal period from hereon), and two afterwards (October 2004 and January 2005). Fruits in one species/density combination were placed in eleven 1 m^2 plots/grid, with densities of 1, 2, 3, 4, 6, 8, 12, 16, 24, 32, and 48/m^2. The plots were randomly selected and located approximately in the middle of a 49 m^2 cell demarked by a trap station at each corner. The number of fruits removed/day was recorded for five consecutive days. Plots were replenished daily to maintain a constant starting density over the five day period.

The second experiment ("long-term" from hereon; Table 2) was conducted in each of four time periods; one prior to density reduction of *H. desmarestianus* (February–April 2004), one during the period of density reduction (July–September 2004; removal period from hereon), and two afterwards (October 2004–January 2005 and January–April 2005). The same fruit densities and arrangements used in the short-

Table 2 Species of trees used in fruit removal experiments in the Bladen Nature Reserve, January 2004–March 2005. Sample size for estimation of fruit weight (mean ± 1 SE) was N=100. For fruiting season, the dry season typically occurs from February to May. Numbers in the cells for short-term (Short) experiments correspond to: Period 1 – 2 February–6 February 2004; Period 2 – 1 May–12 May 2004; Period 3 – 11 June–30 June 2004, Period 4 – 13 October–23 October 2004, and Period 5 – 22 January–26 January 2005. Numbers in the cells for long-term (Long) experiments correspond to: Period 1 – 6 February–1 May 2004; Period 2 – 15 June–12 September 2004; Period 3 – 17 October 2004–20 January 2005, and Period 4 – 21 January–29 April 2005. Numbers in parentheses under Fruit Type and Family are the average number of seeds per fruit

Species	Fruit type and Family	Weight (g)	Fruiting Season	Short	Long
Astrocaryum mexicanum	nutlet (1) Arecaceae	17.4 (0.5)	year-round	1,2,3,4,5	1,2,3,4
Brosimum alicastrum	false drupe (1) Moraceae	2.2 (0.1)	late dry-early wet	2,3	2
Calophyllum brasiliense	drupe (1) Clusiaceae	8.0 (0.3)	late dry-early wet	2,3	2
Chrysophyllum venezuelanense	berry (2) Sapotaceae	3.5 (0.1)	late dry-early wet	2	2
Eugenia aeruginea	berry (10) Myrtaceae	1.9 (0.1)	early wet-mid wet	4	3
Guarea grandifolia	capsule (20) Meliaceae	1.7 (0.2)	late dry		2
Manilkara chicley	berry (3) Sapotaceae	13.4 (0.3)	early dry	1,5	
Quararibea funebris	nut (1) Malvaceae	6.9 (0.1)	early-mid dry	1,2,5	1,4
Spondias mombin	drupe (1) Anacardiaceae	8.6 (0.3)	mid wet	4	3

term experiment were used in the long-term experiment, but removed fruits were not replaced. Plots with nuts of the palm *Astrocaryum mexicanum* were checked at 1–2 day intervals for 90 days, while plots with the other species were checked at 1–2 intervals for 60 days. The number of fruits that were removed was recorded at each visit, as well as the number of seeds that had germinated.

Fruits from eight tree species were used in each of the experiments (nine species total). The species used in each experiment and period are listed in Table 2. Selection of these species was based on fruiting phenology, fruit availability and known or presumed use by *H. desmarestianus* (Brewer and Rejmánek 1999; Klinger and Rejmánek 2009). Because of natural fruiting phenology, *A. mexicanum* was the only species that could be used in all periods for both experiments. In the short-term experiment two species besides *A. mexicanum* were used in the periods immediately prior to and during removal of *H. desmarestianus*; the other five species were used in the periods preceding or following removal (Table 2). In the long-term experiment four species besides *A. mexicanum* were used during the removal period; one species was used both prior to and after the removal period and the other two species after the removal period (Table 2).

Fate of removed fruits was estimated with a spool and thread method (Klinger and Rejmánek 2009, 2010). One to six fruits of each species were threaded with nylon carpet string (length = 135 m per spool), placed in the seed removal plots, then checked every 3–5 days. Fruits were classified as eaten (string only found), taken into a burrow, or cached (surface or buried in leaf litter). If a string was found with a knot left on it and there was no evidence of consumption (fruit parts such as skin or seed fragments) then it was assumed the string had pulled through the fruit and fate was classified as undetermined. The distance and compass bearing of each fruit from its source and the number of fruits in the pile it was taken from were also recorded. Cached fruits were marked with a stake flag and monitored for either one month (species other than *A. mexicanum*) or three months (*A. mexicanum*). At the end of the monitoring period they were classified as germinated, dead (rotted, desiccated, or insect destruction), or missing.

Three cameras connected to infrared motion sensors (TrailMaster Model 1550[tm]) were set above the seed plots to identify the species removing the fruits. One camera/seed plot was set for 2–3 days then moved to another seed plot.

Fruit Removal and Germination Experiments

Germination rates of *Astrocaryum mexicanum*, *Brosimum alicastrum*, *Eugenia aeruginea*, *Quararibea funebris*, and *Spondias mombin* were estimated in twelve 4 m² plots. The plots had dimensions of 4 m × 1 m and were divided into two randomly selected subplots; one subplot enclosed by wire screening (mesh = 0.65cm) and the other left unscreened. The wire screen was buried 4 cm to reduce the likelihood of small mammals entering the enclosure. Two plots were located at random locations in each grid. One hundred fruits of one species were scattered in each enclosed and open part of the plots. Fruits of *B. alicastrum*, *E. aeruginea*, *Q. funebris*, and *S. mombin* would rot or become infested with bruchid beetle larvae if they did not germinate within a month; therefore they were checked for germination at three-day intervals for 30 days. *A. mexicanum* nuts can germinate three months or more after dropping (R. Klinger, pers. observation), so they were checked at weekly intervals for 90 days.

Data Analysis

Density of H. desmarestianus

Population size (N) of *H. desmarestianus* was estimated in the control and DR grids each primary period. Population size was standardized as density (D; individuals/ha), $D = N/A_e$, where A_e = the effective trapping area of the grid (= 0.6 ha). A_e was estimated by the mean maximum distance moved between traps (Wilson and Anderson 1985).

With the exception of the DR grids from May–September 2004, all of the density estimates were based on the robust design model (Pollock et al. 1990). The goodness-of-fit of the most general model and the best starting model were determined in a preliminary analysis using the software program RDSURVIV (Kendall et al. 1997). After goodness-of-fit was tested and a best starting model determined, program MARK was used to estimate N (Cooch and White 2002). Akaike's Information Criterion (AIC) was used to evaluate the set of candidate models, and estimates of N were derived by model averaging for candidate models with ΔAIC <7 (Burnham and Anderson 2002).

Density estimates in the DR grids from May–September 2004 were derived from a removal trapping model M_{hb} (Otis et al. 1978). Program CAPTURE was used to estimate N for the removal trapping (Rexstad and Burnham 1991). Simple linear regression was used to evaluate if the assumption of a linear declining number of captures was met.

Fruit removal and germination rates

Generalized linear mixed models (GLMM's) (Zuur et al. 2009) with a binomial error structure and logit link were used to analyze the proportion of fruits removed/plot/day for species used in multiple time periods of the short-term experiment (*A. mexicanum*, *B. alicastrum*, *Calophyllum brasiliense*, *M. chicle*, and *Q. funebris*) and for species that could only be used in one time period (*Chrysophyllum venezuelanense*, *E. aeriuginea*, and *S. mombin*). Plot was considered a random factor (random intercept) in all analyses. Predictor variables in the GLMM's for multiple time periods were density reduction/non-reduction of *H. desmarestianus* and time period. Predictor variables in the single season GLMM's were density reduction/non-reduction of *H. desmarestianus*. Our primary interest in this study was the overall fruit removal rates per season, therefore we did not include density as a predictor variable in these analyses.

Initial fate of threaded fruits was pooled into two categories; eaten (eaten + burrow) and cached (surface + buried). We then used GLMM's to analyze differences in the proportion of fruits that were eaten. When the proportion of eaten fruits was tracked in multiple seasons, predictor variables in the model included period (N=4 for *A. mexicanum*; N=2 for *Q. funebris*) and removal of *H. desmarestianus*. Predictor variables in the models for species whose fate was tracked in a single season included species (*B. alicastrum*, *Calophyllum brasiliense*, *Chrysophyllum venezuelanense*, *E. aeriuginea*, and *S. mombin*) and removal of *H. desmarestianus*. Plot was considered a random factor (random intercept) in all models.

Generalized linear models (GLM's) (Zuur et al. 2009) were used to analyze the proportion of cached fruits that germinated. The fruits were coded as either having seeds that germinated (=1) or not (=0). Missing seeds were excluded from the analysis because it was impossible to be sure if they had been eaten or cached elsewhere. Sample sizes for cached fruits other than *A. mexicanum* were relatively low so counts were pooled among those species and analyzed separately from *A. mexicanum*. The tradeoff of pooling was a loss in ability to evaluate species-specific patterns. Our more general goal though was to quantify the degree to which germination varied among fruits that were buried and those that were not, and it has long been recognized that burying enhances seed survival and germination (Jansen and Forget 2001). Predictor variables in the models included type of caching (surface or buried) and distance from source where a seed was deposited.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare the relative support for the GLMM and GLM sets. Each set consisted of a null model (intercept only) and models with interactive and additive combinations of the predictor variables (N=5 models). The small sample corrected version of AIC (AICc) was used to rank the models, and the model with the greatest AICc weight (AICc$_w$) was selected as the one with the greatest level of support.

The Kaplan-Meier estimator (Kleinbaum 1996) was used to analyze fruit removal rates in the long-term experiments. Fruit density was pooled within experimental conditions (reduction/non-reduction of *H. desmarestianus*) for each species. Log-rank tests were used to test differences between the two experimental conditions for each species within periods (Kleinbaum 1996).

Log-ratio chi-square tests (Christensen 1997) were used to analyze: (1) differences in the proportion of fruits in the long seed removal experiments that were not removed and germinated; (2) the proportion of fruits removed from open and closed exclosures in control and DR grids; and, (3) the proportion of fruits at the exclosures that were not removed and germinated. Analyses of germination in the long seed removal experiment were done for each species within each period. Species were analyzed individually for the exclosure experiments.

All analyses were done with R version 2.15.1 (R Development Core Team 2012).

Results

Abundance of H. desmarestianus

A total of 843 *H. desmarestianus* were captured during the study. Of these, 799 were captured 2,370 times outside of the removal period (mean capture rate = 2.97/individual). The most general robust design model provided a good fit to the data (*G*=857.37, d.f.=1052, *P*=0.999). The best robust design model included time variation in survival, capture probability, recapture probability, and constant and equal probabilities for immigration and emigration.

Density of *H. desmarestianus* in the control grids increased from 26/ha in January 2004 to 68/ha in August 2004, then declined to 48/ha in December 2004 (Fig. 1). Following the decline, density increased to 72/ha in March 2005. Capture probabilities ranged from 0.29 to 0.67, and recapture probabilities from 0.38 to 0.51.
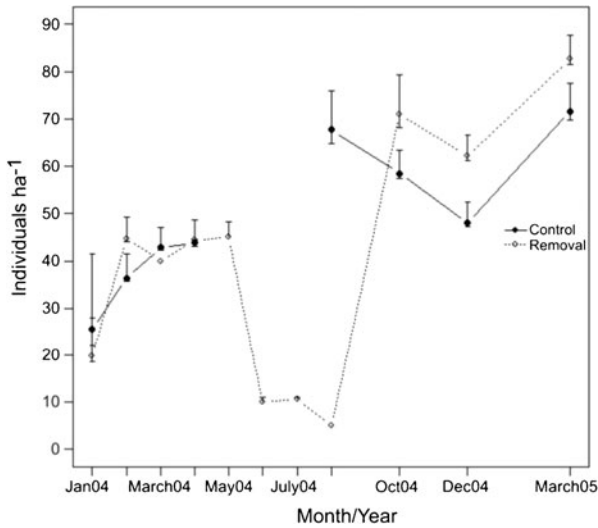
Fig. 1 Density of *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Removals were grids where all *H. desmarestianus* individuals captured between the end of May 2004 and the middle of August 2004 were removed. Controls were grids where abundance of *H. desmarestianus* was allowed to fluctuate naturally

A total of 138 individuals were captured in the DR grids from May–August 2004. There was a significant linear decline in captures during the removal periods (r=0.930, F=146.89, d.f.=1, 23, P≤0.0001). Trapping in the DR grids reduced the density of *H. desmarestianus* from 45/ha to 5–10/ha from June to August 2004. Their abundance in the other months showed a very similar pattern as that in the control grids (Fig. 1).

Short Fruit Removal Experiments

Species used during removal period

The mean proportion of fruits taken/day in the DR grids was either significantly greater or not significantly different from control grids for *A. mexicanum*, *B. alicastrum*, and *Calophyllum brasiliense* in all periods except the removal period (Fig. 2a–c; Table S1 in Electronic Supplementary Material). During the removal period the mean proportion of fruits taken/day for each of those three species was significantly lower in the DR grids (Fig. 2a–c; Table S1 in Electronic Supplementary Material). Fruit removal rates during the removal period were 10 to 19 times greater in the control grids than in the DR grids.

Species used outside of removal period

The mean proportion of fruits taken/day for *Q. funebris* and *M. chicle* was either significantly greater in DR grids or not significantly different from control grids in each period (Fig. 2d–e; Table S1 in Electronic Supplementary Material). There was no significant difference in fruit removal rates between control and DR grids for *E. aeriuginea* and *S. mombin*. The mean proportion of fruits taken/day was significantly

greater in DR grids for *Chrysophyllum venezuelanense* (Fig. **2f**; Table **S1** in Electronic Supplementary Material).

Long Fruit Removal Experiments

Fruits of *A. mexicanum* were removed at higher rates in the DR grids than the controls prior to the removal period (Table **3** and Fig. **3a**). Fruits of *Q. funebris* were taken at higher
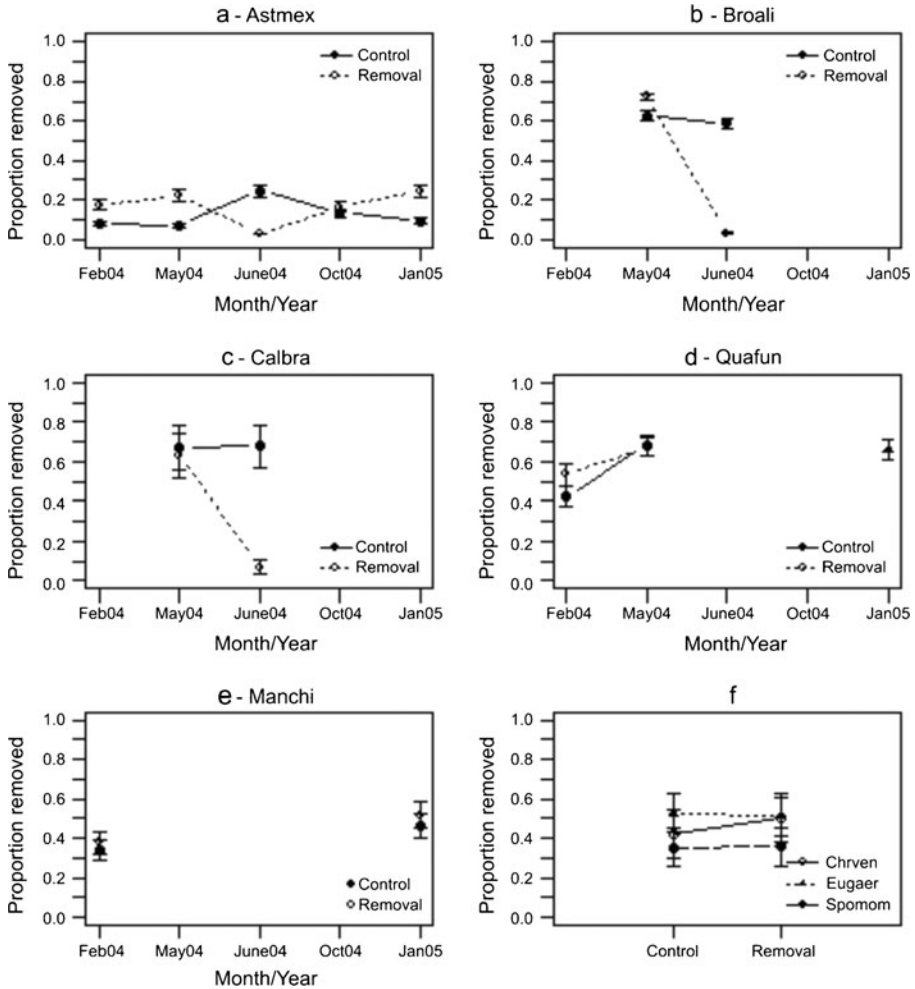

Fig. 2 **a–c** The mean proportion of fruits removed/day for three species of tree in the Bladen Nature Reserve, Belize. Condition is whether *Heteromys desmarestianus* was removed (Removal – dashed lines) from grids or not (Control – solid lines) from the end of May to mid-August 2004. The experiment was conducted for five consecutive days in each month. Fruit removal experiments in May 2004 were completed before removal of *Heteromys desmarestianus* was initiated. Fruit removal experiments in June 2004 were completed while removal of *Heteromys desmarestianus* was ongoing. **d–f** As in **a–c** except the experiments were done in multiple periods (**d–e**) or in a single period (**f**) for tree species with fruiting phenology outside of the removal period for *Heteromys desmarestianus*. Species codes: Astmex – *Astrocaryum mexicanum*, Broali – *Brosimum alicastrum*, Calbra – *Calophyllum brasiliense*, Quafun – *Quariribea funebris*, Manchi – *Manilkara chicle*, Chrven – *Chrysophyllum venezuelanense*, Eugaer – *Eugenia aeruginea*, Spomom – *Spondias mombin*

Table 3 Total percent removal of fruits and the percent germination of seeds of eight species of trees in the Bladen Nature Reserve, Belize. χ^2 is the log-ratio test statistic for differences in fruit removal curves between grids where density of *Heteromys desmarestianus* was reduced for three months (June–August 2004) and grids where density was unmanipulated (Removal and Controls, respectively). Species codes are: Astmex – *Astrocaryum mexicanum*, Broali – *Brosimum alicastrum*, Calbra – *Calophyllum brasiliense*, Chrven – *Chrysophyllum venezuelanense*, Eugaer – *Eugenia aeruginea*, Guagra – *Guarea grandifolia*, Quafun – *Quariribea funebris*, and Spomom – *Spondias mombin*. Empty cells resulted from complete fruit removal

Species	Season	Fruits/Removed (%)		χ^2	*P*	Germination (%)			
		Control	Removal			Controls	N	Removal	N
Astmex	Jan–Apr 2004	91.5	96.0	133.25	0.0001	0.6	3	0.0	0
Astmex	June–Aug 2004	95.3	60.5	709.29	0.0001	0.2	1	5.8	27
Astmex	Oct–Dec 2004	74.1	73.7	0.41	0.5240	3.0	14	3.6	17
Astmex	Jan–Apr 2005	84.0	87.0	5.07	0.0240	1.5	7	1.1	5
Broali	June–Aug 2004	100.0	77.2	596.99	0.0001			3.7	12
Calbra	June–Aug 2004	100.0	86.1	766.61	0.0001			0.9	3
Chrven	June–Aug 2004	50.3	23.1	64.24	0.0001	6.2	20	11.4	37
Eugaer	Oct–Dec 2004	100.0	100.0	0.14	0.7060				
Guagra	June–Aug 2004	22.8	22.2	0.07	0.7710	8.9	29	10.2	33
Quafun	Jan–Apr 2004	100.0	100.0	26.90	0.0001				
Quafun	Jan–Apr 2005	100.0	100.0	219.92	0.0001				
Spomom	Oct–Dec 2004	63.9	56.2	11.27	0.0001	1.2	4	1.9	6

rates in the control than the DR grids prior to the removal period (Table 3), but the difference in rates was only in the first 3–4 days (Fig. 3i). After that the shapes of the curves were very similar and all the fruits were taken within 11−12 days in all the grids (Table 3 and Fig. 3i). During the removal period the fruit removal rates for *A. mexicanum*, *B. alicastrum*, *Calophyllum brasiliense*, and *Chrysophyllum venezuelanense* were significantly higher in control than in DR grids (Table 3). Fruit removal rates in the DR grids were low for all four species during the first 30 days of the removal period (July to mid-August 2004); the rate of fruit removal increased after mid-August when removal trapping of *H. desmarestianus* had stopped (Fig. 3b,e,f, and g). In the control grids, fruits of *B. alicastrum* and *Calophyllum brasiliense* were completely removed within 20–30 days (Fig. 3e and f). There was no significant difference between control and DR grids for seed removal rates of *G. grandifolia* during the removal period (Table 3 and Fig. 3h). Only 22 % were taken in this period and their removal rate and total proportion removed were very low compared to the other species.

There was no significant difference in fruit removal rates between control and DR grids for *A. mexicanum* and *E. aeruginea* after the removal period (Table 3 and Fig. 3c,d, and k). All fruits of *E. aeruginea* were removed in all grids within 20–25 days (Fig. 3k). The removal rate of *S. mombin* fruits was significantly greater in the DR grids after the removal period (Table 3i). Removal rate curves were similar between control and DR grids (Fig. 3i), but mean removal time for fruits in the DR grids was 29 days while in control grids it was 44 days. Overall, the difference in the total proportion of *S. mombin* fruits taken from the control and DR grids was only 7.7 % (Table 3).
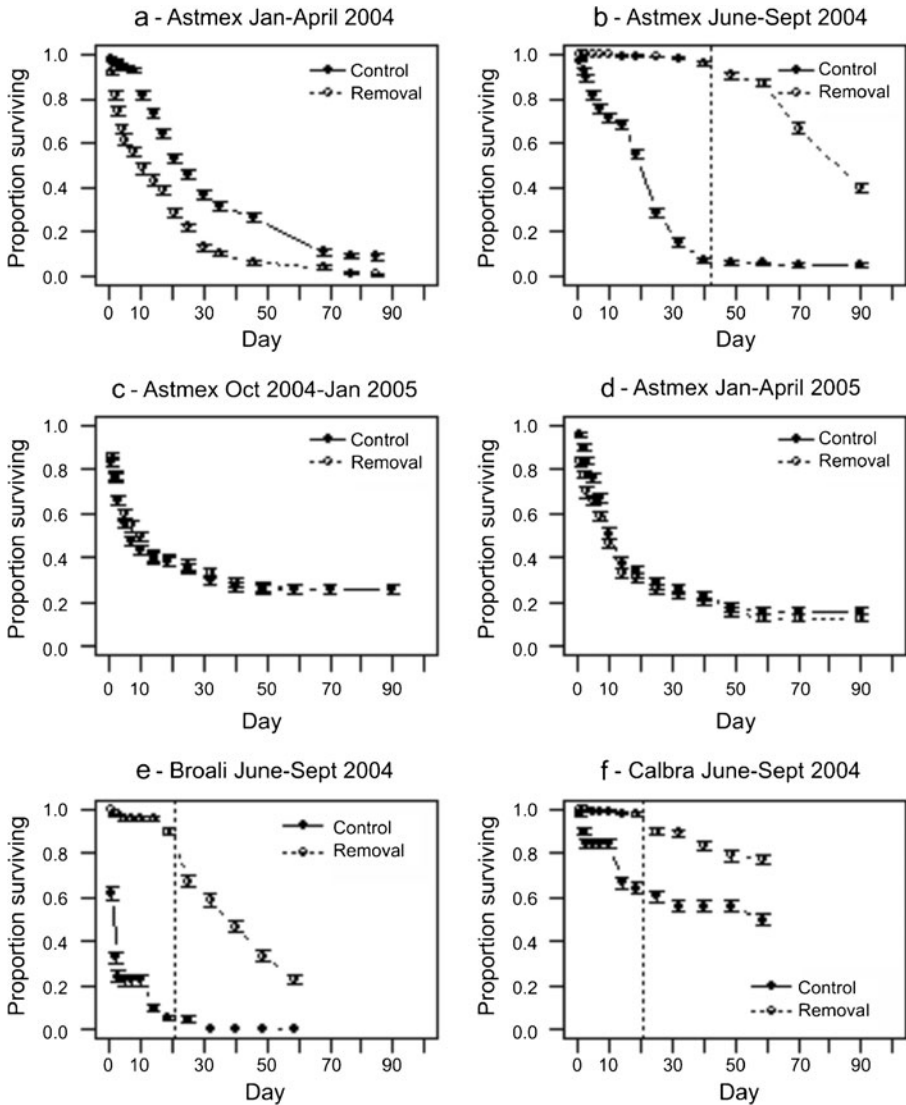
Fig. 3 The proportion of fruits remaining for eight species of trees across four fruiting periods in the Bladen Nature Reserve, Belize. Abundance of *Heteromys desmarestianus* was experimentally reduced in three of six trapping grids from May–August 2004 but was not manipulated January–April 2004, October 2004–January 2005, or January–April 2005. Species codes are: Astmex – *Astrocaryum mexicanum*, Broali – *Brosimum alicastrum*, Calbra – *Calophyllum brasiliense*, Chrven – *Chrysophyllum venezuelanense*, Eugaer – *Eugenia aeruginea*, Guagra – *Guarea grandifolia*, Quafun – *Quariribea funebris*, and Spomom – *Spondias mombin*. Removed refers to whether *Heteromys desmarestianus* was removed (dashed lines – Removal grids) from grids or not (solid lines – Control grids). The vertical dashed line in the June–September 2004 period is when removal trapping ceased.

Fruit removal rates were significantly higher in DR than control grids for *A. mexicanum* from January–April 2005 (Table 3). However, these differences were relatively minor; the curves for each species were very similar between control and DR grids (Fig. 3d) and the difference in the total proportion removed was only 3 %.
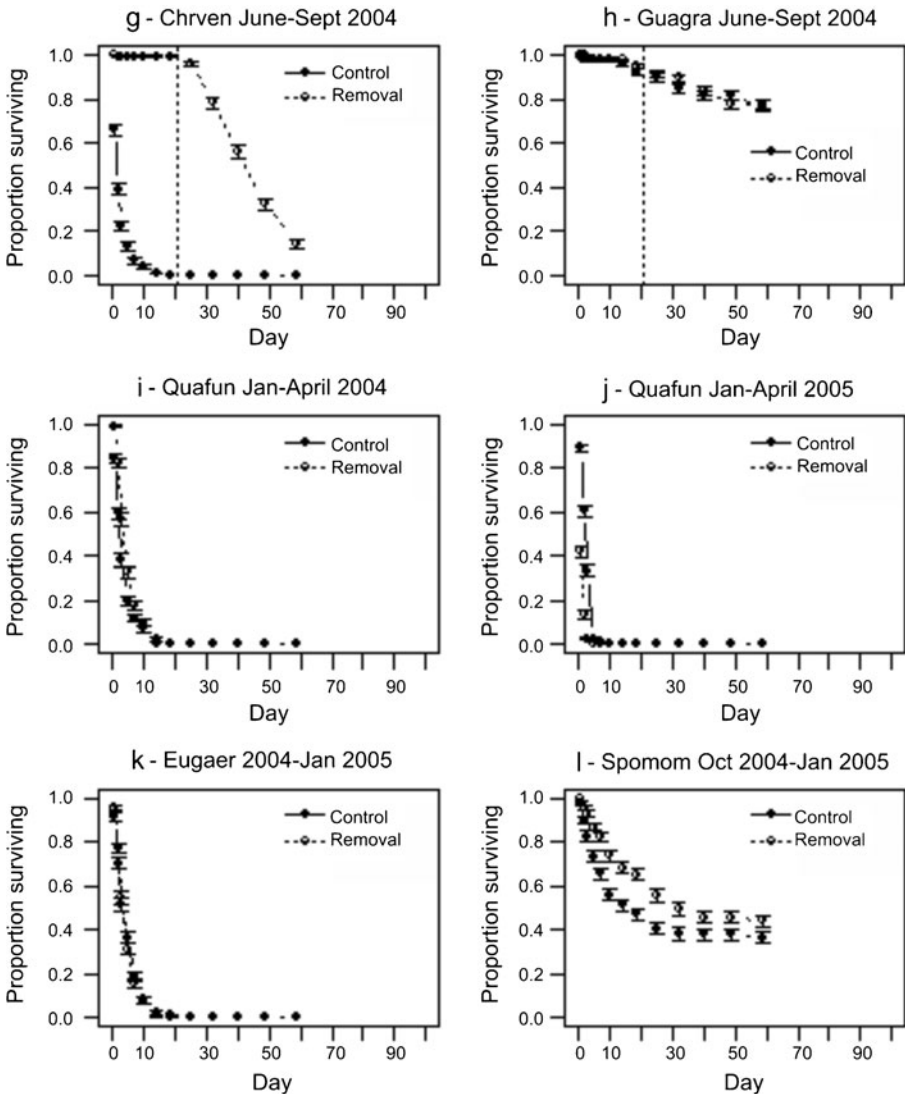
Fig. 3 (continued)

Fruit removal rates of *Q. funebris* were very similar. All fruits were removed within 5–10 days.

The proportion of seeds that germinated out of the total starting number (N=468 per species per experimental condition) was significantly greater in the DR grids during the removal period for *A. mexicanum*, *B. alicastrum*, *Calophyllum brasiliense*, and *Chrysophyllum venezuelanense* ($0.001 \leq P \leq 0.041$; Table 3). There was no significant difference between control and DR grids for the proportion of seeds germinating out of the total starting number for *G. grandifolia* and *S. mombin*, or *A. mexicanum* in the other periods ($P \geq 0.522$). Germination of the seeds remaining at the end of each long seed removal experiment was not associated with control and DR grids for any

species (0.484≤*P*≤0.736; Table 3). Germination rates of the remaining seeds ranged from 7.5 % to 16.9 % (N=1–37; Table 3).

H. desmarestianus was the only species identified in photographs of fruits being removed (N=38). Movement patterns of the strung fruits under low vegetation and into burrows provided additional evidence that *H. desmarestianus* was responsible for removal of all fruits used in the experiments.

Seed Fate

Fates of 919 threaded fruits were determined during the study. This included: 411 *A. mexicanum*, 61 *B. alicastrum*, 71 *Calophyllum brasiliense*, 76 *Chrysophyllum venezuelanense*, 96 *E. aeriuginea*, 119 *Q. funebris*, and 85 *S. mombin*.

Proportion eaten

The model of the proportion of fruits eaten that included the interaction between species identity and reduction in density of *H. desmarestianus* had overwhelming support (AICc$_w$=1) in the analysis where the six species were pooled. This was because 10 % fewer fruits of *Calophyllum brasiliense* were consumed in the removal plots (80.9 %) than in the control plots from June−August 2004, whereas a similar proportion of fruits of the other four species were consumed among control and removal plots. The percentage of fruits of *B. alicastrum* and *Chrysophyllum venezuelanense* that were eaten ranged from 85.6 % to 91.5 % (June–August 2004). The percentage of fruits of *E. aeriuginea* and *S. mombin* that were eaten ranged from 82.9 % to 85.4 % (October–December 2004). In general, there was no significant relationship between the proportion of seeds eaten and reduction in density of *H. desmarestianus* (*P*=0.288).

The model of the proportion of fruits eaten for *Q. funebris* that included the interaction between period (February–April 2004 and February–April 2005) and reduction in density of *H. desmarestianus* had overwhelming support (AICc$_w$=1). Virtually all fruits (99 %) were eaten in the removal plots during both periods, while 92.5 % (± 1.1 % SE) and 84.3 % (± 4.9 % SE) were eaten in the control plots during both periods.

The model of the proportion of fruits eaten for *A. mexicanum* that included the interaction between period and reduction in *H. desmarestianus* density also had overwhelming support (AICc$_w$=1). The mean percentage of *A. mexicanum* nuts eaten per period in the control grids varied between 82.2 % and 94.4 %, but in the DR grids it decreased to 37.2 % from June–August 2004 (Fig. 4). However, only seven threaded *A. mexicanum* nuts were taken in the DR grids from June–August 2004, so the consumption rate during that period must be interpreted cautiously.

Proportion germinating

Over half of the 123 threaded seeds that were cached died (52 %), but 24.4 % germinated. In general germination rates were strongly distance-dependent; 77 % of the seeds dispersed ≤5m did not germinate while 80 % of those that were dispersed >5 m did.

Each of the models that included both caching mode and distance from source for the proportion of *A. mexicanum* seeds that germinated had support (interaction model AICc$_w$=0.65; additive model AICc$_w$=0.25), therefore we used model averaging
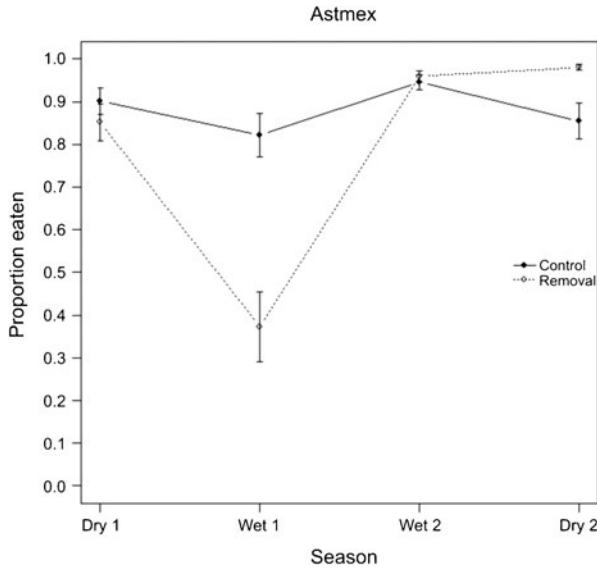
Fig. 4 The proportion of threaded *Astrocaryum mexicanum* nutlets eaten during four sampling periods in the Bladen Nature Reserve, Belize. Periods are: Dry 1 – February–May 2004; Wet 1 – June-September 2004; Wet 2 – October 2004–January 2005; Dry 2 – February–April 2005. The density of *Heteromys desmarestianus* was reduced by >90 % in half of the 0.5 ha plots (Removal; N=3) from June–August 2004

(Burnham and Anderson 2002) for parameter estimation. All *A. mexicanum* seeds were cached within 8 m of their source. Germination of buried seeds was consistently greater than those on the surface, particularly between 0.5m and 5 m from their source (Fig. 5a). Half of the *A. mexicanum* seeds were dispersed <1.5 m and 77 % <2 m.

The model that included the interaction between caching mode and distance from source pile for the proportion of seeds that germinated for the six pooled species had
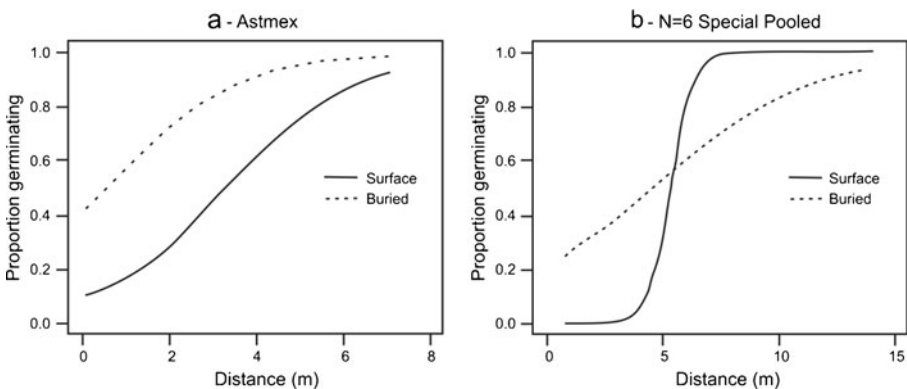

Fig. 5 Model based estimates of the proportion of threaded fruits removed from experimental fruit piles, cached and then germinated pooled across four time periods in the Bladen Nature Reserve, Belize. The periods were: February–May 2004, June-September 2004, October 2004–January 2005, February–April 2005. The density of *Heteromys desmarestianus* was reduced by >90 % in half of the 0.5 ha plots (N=3) from June-August 2004. In panel (**a**) Astmex – *Astrocaryum mexicanum*. The six species whose rates were pooled because of low sample sizes were *Brosimum alicastrum*, *Calophyllum brasiliense*, *Chrysophyllum venezuelanense*, *Eugenia aeruginea*, *Quariribea funebris*, and *Spondias mombin* (**b**)

very strong support (AICc$_w$=0.89). All seeds were cached within 15 m of their source. Seeds that were buried within 5 m of the source pile had much greater rates than those left on the surface, but the relationship switched at distances greater than 5 m (Fig. 5b). The distribution of the seeds was strongly right-skewed, with 61 % of the seeds dispersed <2 m and 84 % <5 m. The odds ratio for a cached seed germinating the greater the distance from its source was 1.55 (95 % CI 1.22–1.97; $P \leq 0.0001$).

Fruit Removal and Germination Experiments

No seeds were removed from enclosed plots in either control or DR grids. In the open plots, the proportion of seeds removed in control and DR grids did not vary significantly among the species in either period ($P \geq 0.636$). A total of 969 fruits were taken during the removal period; 8.5 % were from the DR grids. There were 1362 fruits taken after the removal period; 50.8 % were taken from the DR grids (χ^2=513.613, d.f.=1, $P \leq 0.0001$). All *B. alicastrum* and *Q. funebris* fruits in open plots in the control grids were removed within 10 days. All *E. aeruginea* fruits in open plots in the control and DR grids were removed within 18 days.

A total of 394 seeds germinated in the in the 4 m^2 exclosures. The proportion that germinated varied significantly between periods, density reduction of *H. desmarestianus*, and exclosures (χ^2=34.244, d.f.=1, $P \leq 0.0001$). During the removal period 97 % of the seeds that germinated in open plots were in DR grids; 44 % germinated in open plots in the DR grids after the removal period (χ^2=44.65, d.f.=1, $P \leq 0.0001$; Table 4). In the enclosed plots there was no significant difference in germination rates between control and DR grids during the removal period (χ^2=0.048, d.f.=2, P=0.926) or in the three months afterwards (χ^2=1.442, d.f.=2, P=0.486).

Discussion

Seed limitation is only one of several mechanisms influencing recruitment of plants. We focused on the early stages of a plants life history, and it is likely that establishment limitation (Table 1) also plays a very important role in the survival of seedlings and saplings (Muller-Landau et al. 2002; Schupp et al. 2002). Moreover, the strength of establishment limitation could be intensified through disperser mediated processes such as directed dispersal (Hirsch et al. 2012; Spiegel and Nathan 2012). Nevertheless, at the seed stage, germination rates of many trees in the BNR were determined by both predation limitation and seed dispersal.

We were not able to trap in the control grids during the period when density of *H. desmarestianus* was reduced, but there is little if any likelihood that their abundance in the control grids crashed during the removal period. Density of *H. desmarestianus* does have seasonal fluctuations and this appears to be related to food availability, but unless there is a major disturbance their population typically ranges from 30 to 70 individuals per ha (Klinger 2007).

Reducing density of *H. desmarestianus* resulted in an order of magnitude decrease in fruit removal rates and an order of magnitude increase in the proportion of seeds that germinated. Because of natural fruiting phenology we could only compare rates

Table 4 Germination (%) of seeds of five species of trees in 4 m^2 plots in the Bladen Nature Reserve, Belize. Density of *Heteromys desmarestianus* was reduced from May–August 2004 in three of six 0.50 ha grids; abundance in the other grids was not manipulated (controls). Two plots (4 m × 1 m) were established in each grid and 100 seeds placed in one half of each that was either fenced (Closed) or unfenced (Open). Percentages are based on N=300 seeds/species. Statistics are log-likelihood χ^2 ratio tests

Plot	Density of *Heteromys desmarestianus*	
	Control	Reduced
June−August 2004		
Astrocaryum mexicanum: χ^2=12.73, 1 d.f., *P*=0.0001		
Closed	7.70	8.70
Open	1.30	8.33
Quararibea funebris: χ^2=31.73, 1 d.f., *P*=0.0001		
Closed	10.00	11.70
Open	0.00	11.30
Brosimum alicastrum: χ^2=27.44, 1 d.f., *P*=0.0001		
Closed	7.70	8.30
Open	0.00	9.70
September−December 2004		
Astrocaryum mexicanum: χ^2=0.17, 1 d.f., *P*=0.6810		
Closed	5.0	5.30
Open	4.7	4.00
Eugenia aeruginea: χ^2 = 0.00, 1 d.f., *P* = 1.0000		
Closed	9.70	8.70
Open	0.00	0.00
Spondias mombin: χ^2=1.42, 1 d.f., *P*=0.2330		
Closed	2.30	4.00
Open	2.00	1.30

of seed predation and dispersal for five of the nine tree species during the period when density of *H. desmarestianus* was reduced. Even so, the strikingly high removal rates for fruits of the other four species in periods when density of *H. desmarestianus* was not reduced were consistent with those in the control grids when density of *H. desmarestianus* was reduced. The only period of time when fruit removal rates were consistently low was when *H. desmarestianus* was removed. This was especially apparent after removal of *H. desmarestianus* ceased in August 2004, and for *A. mexicanum*, the only species whose fruits were available in all periods of the study.

Large and medium-sized mammals known to be important seed predators or dispersers (e.g. *Tayasu tajacu, Dasyprocta punctata, Agouti paca*) occur in the BNR, but they were uncommon in the region where the study was done (R. Klinger and S. Brewer, unpubl. data). In addition, at least nine other small mammal species occur in the study area (Klinger 2006). However, there was no evidence that any other mammal species compensated for the reduction in density of *H. desmarestianus* by exploiting the same food resources. The broad dietary breadth of *H. desmarestianus* (Martinez-Gallardo and Sánchez-Cordero 1993), its abundance, and apparent lack of

functional redundancy in the small mammal assemblage in the BNR strongly suggests *H. desmarestianus* has a critical, year-round participation in seed predation and dispersal for many tree species in the BNR.

Although seed predation was a strong limiting factor on germination of some of the tree species, *H. desmarestianus* dispersed and cached about 10 % of the fruits they handled. Most of the cached seeds died, but approximately 25 % germinated. This was 2 to 3 times greater than the germination rates of undispersed seeds, and for *B. alicastrum* and *Q. funebris* dispersed seeds were the only ones that germinated. In addition, the odds of a seed germinating increased the farther it was cached from its source, which is consistent with predictions of the escape hypothesis (Janzen 1970; Connell 1971). Although most seeds were cached within 3–5 m of where they were placed, others were cached two to three times further away. While longer-distance caching may only occur infrequently, these seeds may have a disproportional importance on recruitment patterns (Muller-Landau et al. 2002), particularly in systems where seed dispersers may move seeds many times and at increasing distances from the parent plant (Jansen et al. 2012).

Germination rates varied with fruit consumption rates, suggesting that the strength of seed limitation can often vary considerably among tree species. High rates of predation resulted in virtually no germination for those fruits that *H. desmarestianus* showed an apparently strong diet preference for (*B. alicastrum*, *Calophyllum brasiliense*, *E. aeruginea*, and *Q. funebris*). Germination rates were generally higher for seeds that were less consumed diet items, particularly *Chrysophyllum venezuelanense* and *G. grandifolia*. This suggests that there will be a distribution of seed limitation strengths within a community. The distribution would likely be unimodal when seed limitation is mediated by a single seed predator species, with the shape of the distribution determined by the diet preference of the seed predator. However, the distribution could assume a variety of shapes when multiple seed predators were exploiting the same resource base. For example, in seed predator assemblages where species have high dietary overlap but different preferences the distribution could be relatively uniform.

It is recognized that the influence dispersal has on diversity varies with spatial scale (Cadotte 2006), and a great deal of emphasis has been placed on the importance of spatial patterns of seed dispersal (Schupp and Fuentes 1995; Nathan and Muller-Landau 2000). However, temporal variation in the strength of seed limitation may often be important as well (Wright 2002), and patterns in spatial distribution of trees could potentially result from strong temporal dynamics in seed predation and dispersal rates. Fluctuations in abundance of seed predator populations are common in tropical forests, which could result in a switch in importance of predation limitation and dispersal limitation (Curran and Leighton 2000; DeMattia et al. 2004; Klinger and Rejmánek 2009). For example, in years when seed predator numbers are high, germination and seedling recruitment could be suppressed by high rates of seed predation. This pattern would be consistent with predation limitation and was what we observed in the BNR during this study. However, relatively low seed removal and dispersal rates of *A. mexicanum* in the BNR occurred when abundance of *H. desmarestianus* decreased in the year after a hurricane, whereas they had been relatively high before (Klinger and Rejmánek 2009). This suggests that, at least in the BNR, the relative importance of predation and dispersal limitation can shift spatially and temporally and will often be linked to abundance of *H. desmarestianus*.

Conclusions

A number of studies have emphasized that the relative importance of recruitment limitation and seed dispersal determines diversity and spatial distribution of plants in temperate and tropical ecosystems (Turnbull et al. 2000; Webb and Peart 2001; Orrock et al. 2006; Blendinger and Diaz-Velez 2010). While this is certainly true in many cases, our results indicate a far more complicated relationship between the two processes; both can occur simultaneously and they are not necessarily independent of one another. Seed addition studies and analysis of seedling composition in plots provide support for the occurrence and importance of seed limitation, but they are essentially snapshots of much more complex interactions. Few studies have directly examined seed limitation dynamics, especially as they relate to the often substantial variation in abundance of seed disperser populations or composition of disperser assemblages. For tree species with animal-mediated seed dispersal, the dynamics of seed predator/disperser populations may frequently be a crucial link with observed recruitment and spatial distribution patterns.

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