A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm

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Abstract Seed predation and seed dispersal can have strong effects on early life history stages of plants. These processes have often been studied as individual effects, but the degree to which their relative importance co-varies with seed predator abundance and how this influences seed germination rates is poorly understood. Therefore, we used a combination of observations and field experiments to determine the degree to which germination rates of the palm Astrocaryum mexicanum varied with abundance of a small mammal seed predator/disperser, Heteromys desmarestianus, in a lowland tropical forest. Patterns of abundance of the two species were strongly related; density of H. desmarestianus was low in sites with low density of A. mexicanum and vice versa. Rates of predation and dispersal of A. mexicanum seeds depended on abundance of H. desmarestianus; sites with high densities of H. desmarestianus had the highest rates of seed predation and lowest rates of seed germination, but a greater total number of seeds were dispersed and there was greater density of seedlings, saplings, and adults of A. mexicanum in these sites. When abundance of H. desmarestianus was experimentally reduced, rates of seed predation decreased, but so did dispersal of A. mexicanum seeds. Critically, rates of germination of dispersed seeds were 5 times greater than undispersed seeds. The results suggest that the relationship between A. mexicanum and H. desmarestianus is a conditional mutualism that results in a strong local effect on the abundance of each species. However, the magnitude and direction of these effects are determined by the relative strength of opposing, but related, mechanisms. A. mexicanum nuts provide H. desmarestianus with a critical food resource, and while seed predation on A. mexicanum nuts by H. desmarestianus is very intense, A. mexicanum ultimately benefits because of the relatively high germination rates of its seeds that are dispersed by H. desmarestianus.

Keywords Granivory · Predation limitation · Recruitment limitation · Seed predation

Introduction

Because of their contribution to recruitment limitation, seed dispersal and seed predation are considered two of the most significant processes that determine patterns of regeneration, diversity and spatial structuring in plant communities (Muller-Landau et al. 2002; Schupp et al. 2002). While it is evident that seed dispersal and seed predation have strong population- and community-level effects on plants, it is also becoming increasingly clear that their relative strength can vary widely (Howe and Miriti 2004). In some cases regeneration and spatial pattern of trees may be limited by high rates of seed predation (Silman et al. 2003; Kaufman and Maron 2006; Orrock et al. 2006), in others they may be...
limited by low rates of seed dispersal (Cordeiro and Howe 2003; Makana and Thomas 2004), while in some other cases spatial patterns appear to result from high rather than low rates of seed dispersal (Webb and Peart 2001).

There are several hypotheses on how recruitment is determined by where seeds are dispersed (Wenny 2001; Schupp et al. 2002). In contrast, hypotheses on the relationship between seed survival and the dynamics of seed predator populations are almost entirely ad hoc (but see Nathan and Casagrandi 2004; Adler and Muller-Landau 2005; Mari et al. 2008). In general, the degree to which seed predators influence seed survival will depend in large part on three factors: the species-specific ratio of seeds eaten or dispersed, variation in seed predator abundance, and the degree of overlap in diet in seed predator guilds. Many animal species exploit seeds and most can be considered both seed predators and dispersers, but there is great variability in the proportion of seeds different species disperse. In some cases animals disperse a high enough proportion of seeds of some plant species that the relationship is considered a mutualism (Longland et al. 2001), while in other cases animal species disperse few if any of the seeds they exploit (Beck 2006). Numerous studies have shown that changes in density of seed predator/disperser populations result in shifts in patterns of seed predation and dispersal (Adler and Kestell 1998; Curran and Leighton 2000; Wright et al. 2000; DeMATTia et al. 2004), while the degree of diet overlap in seed predator/disperser guilds determines the overall intensity of seed predation and the extent of seed dispersal. In addition, interactions among these factors could have very different effects on plant distribution and abundance. For instance, changes in seed predator abundance may not necessarily influence distribution of a plant species but it could have a major influence on its abundance (Silman et al. 2003; DeMATTia et al. 2004). Alternatively, if the seed predator/disperser guild was composed in large part of species that were primarily seed predators, changes in the composition of the guild could result in changes in both plant distribution and abundance (Kaufman and Maron 2006; Orrock et al. 2006).

In this study we examined the degree to which germination rates of the palm Astrocaryum mexicanum Liebm. ex Mart. (Arecaceae) were determined by seed predation and seed dispersal, and whether the relative rates of seed predation and dispersal varied with alteration in species composition of the seed predator/disperser guild. In the course of previous investigations (Brewer and Rejmánek 1999; Brewer 2001; Klinger 2007; Klinger and Rejmánek 2009) we observed that a large proportion of A. mexicanum nuts were both preyed on and dispersed by the most abundant small mammal in the forest, Heteromys desmarestianus subspp. desmarestianus Gray (Heteromyidae). The spatial patterns of abundance of the two species co-varied and they seemed to have a reciprocal positive effect on each other (R. Klinger and M. Rejmánek, unpublished data). It was likely that A. mexicanum had a strong influence on the abundance of H. desmarestianus because of food availability, but how H. desmarestianus influenced abundance of A. mexicanum was less clear. The population dynamics of H. desmarestianus are driven primarily by food availability, with A. mexicanum nuts being their only year-round food resource (Klinger 2006, 2007). So, in sites where, or during periods when, food availability was high, abundance of H. desmarestianus was also high. But in these sites or during these periods when food availability was high predation on A. mexicanum nuts was also high (Klinger and Rejmánek 2009). Although seed predation by H. desmarestianus seemed to be a major influence on the spatial patterns of A. mexicanum, these patterns could have been due to seed dispersal by H. desmarestianus, high seed predation rates from other mammals, or because some sites were less suitable for germination and growth of A. mexicanum than others.

We hypothesized that seed predation and seed dispersal would have a much greater effect on germination rates of A. mexicanum seeds than abiotic conditions, and that germination rates would be consistently influenced more by seed predation by H. desmarestianus than seed dispersal. To test our hypotheses we compared rates of seed predation, seed dispersal, and germination among sites with varying abundance of A. mexicanum, including three sites where we used removal trapping to reduce the abundance of H. desmarestianus. This allowed us to directly evaluate whether experimental reduction of H. desmarestianus density in sites where density of A. mexicanum was high resulted in patterns of seed predation, seed dispersal and germination similar to sites where density of A. mexicanum was naturally low, and the degree to which seed predation and dispersal of A. mexicanum was compensated by other small mammal species after density of H. desmarestianus was reduced. We expected that: (1) reduction in abundance of H. desmarestianus would result in a significant decrease in seed predation and higher germination rates of A. mexicanum seeds, and (2) germination and initial establishment rates of A. mexicanum seeds would not vary among sites independently of density of H. desmarestianus or other mammal seed predators/dispersers.

**Materials and methods**

**Study area and species**

The study was conducted from January 2004 to March 2005 in a 5-km² section of the Bladen Nature Reserve (BNR), a 350-km² area located within the Maya Mountains in southern Belize (16°33′N, 88°43′W). The Bladen branch
Three cameras connected to infrared motion sensors (TrailMaster model 1550) were moved among the seed plots to identify the mammal species removing the seeds. One camera/seed plot was set for 2–3 days then moved to another seed plot.

Controlled feeding experiments were used to determine consumption of *A. mexicanum* seeds by small rodents. Five *H. desmarestianus* from the DR grids and five adults of each of two murid rodent species, *Ototylomys phyllotis* Merriam and *Sigmodon hispidus* Say & Ord, were used in cafeteria-style feeding trials. *O. phyllotis* and *S. hispidus*
are the only other commonly occurring rodents in the BNR (Klinger 2006) and were captured in arbitrary locations 1 km from the trapping grids.

Each individual was housed in a 16 cm × 5 cm × 5 cm wire cage and maintained with free water and from ten to 15 kernels of whole corn (Zea mays; 5–15 g total) and rolled oats (5–10 g total) provided ad libitum. The feeding trials consisted of removal of the maintenance diet and then providing each of the fifteen individuals with three A. mexicanum seeds (15–18 g each), as well as from ten to 12 whole peanuts (40–45 g total) and three slices of banana or plantain (15–20 g each). The trials were conducted 5 times in July and August 2004, with each trial separated by 3–4 days. The number of A. mexicanum seeds that were consumed was monitored each morning for 3 consecutive days. The peanuts and plantain were included in the trials because some species did not consume the A. mexicanum seeds and required supplemental food (see “Results”). Peanuts and plantain provided food different from that in the maintenance diet, thereby avoiding bias due to habituation to a particular diet but still enabling comparisons to be made among the three species. These protocols were consistent with guidelines and recommendations by the Animal Care and Use Committee at the University of California, Davis.

Seed germination

Seed-removal plots

A. mexicanum seeds that remained in the seed-removal plots were monitored for germination at weekly intervals for 90 days. At the end of each monitoring period the seeds were classified as germinated or dead.

Exclosures

Germination rates of A. mexicanum were estimated from December 2004–March 2005 in nine 4-m² (4 m × 1 m) plots. A single plot was located randomly within each grid. The plots were divided into two randomly selected sides; one enclosed by wire screening and the other left unscreened. The screen was buried to a depth of 4 cm to reduce the likelihood of small mammals entering the enclosure. One hundred A. mexicanum seeds were scattered in each enclosed and open part of the plots and checked for germination at weekly intervals for 90 days. At the end of the monitoring period the seeds were classified as germinated or dead.

Seed fate

Seed fate was estimated with a spool and thread method. One to six seeds were threaded with nylon carpet string, placed in the seed-removal or seed-germination plots, then checked every 3–5 days. Fate was classified as eaten (string only found), taken into a burrow, cached (surface or buried in leaf litter), or undetermined. Cached seeds were marked with a stake flag and monitored for 3 months. At the end of the monitoring period they were classified as germinated, dead, or missing.

Data analysis

Small mammal density

With the exception of the DR grids from May to September 2004, density estimates (individuals ha⁻¹) of H. desmarestianus, Ototylomys phyllotis, and Sigmodon hispidus were derived from the robust design model (Pollock et al. 1990) using program MARK (Cooch and White 2002). Details on model-selection procedures for the density estimates are given in Klinger (2007). Density of H. desmarestianus in the DR grids during the removal trapping period was based on a closed population removal trapping model (M₉₀), using program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991). Ordinary least-squares regression was used to evaluate the assumption of a linear decline in the number of captures for the M₉₀ model. Paired t-tests were used to evaluate differences in density of H. desmarestianus between the flats and the lower slope (≤30 m) and the flats and the mid and upper slopes (>30 m).

Non-linear regression was used to analyze the relationship between elevation above the flats and the distribution of the three small mammal species. The dependent variable was the number of unique individuals captured at each trap station (pooled across time periods). Recaptures of individuals at the same trap were not included to avoid non-independence. The data were fit by a simple exponential equation $e^{a + b \times \text{elevation}}$, where $e$ is the base of natural logarithms, $e^a$ is the intercept, and $b$ the slope parameter. Parameter estimates were obtained by least squares using the Gauss–Newton method and considered to be significant if their 95% confidence intervals did not include zero.

Distribution of A. mexicanum, seed removal, and seed germination rates

One-way multivariate nested ANOVA (MANOVA) was used to test for differences in density of A. mexicanum between sites (flats and slopes). The nested factor was plots within sites. Because the area of the plots differed between flats (0.005 ha) and slopes (0.01 ha), density was standardized as stems per 0.005 ha. The dependent variables were densities (log +1 transformed) of the age classes of A. mexicanum. Non-linear regression was used to analyze the relationship between elevation above the flats and the distribution of adult A. mexicanum. The relationship
between elevation and distribution of *A. mexicanum* saplings and seedlings was not analyzed because of their low abundance on the slopes (see “Results”).

The Kaplan–Meier estimator and log-rank tests (Kleinbaum 1996) were used to analyze differences in removal rates of *A. mexicanum* seeds between sites across the four seasons. Profile analysis (Tabachnik and Fidell 1996) was used to test for differences in the total proportion of *A. mexicanum* seeds removed between the sites across the four seasons. ANOVAs followed by planned comparisons were used to test the difference between sites in the total proportion (after angular transformation) of *A. mexicanum* seeds removed.

Generalized linear models (McCullagh and Nelder 1989) with a binomial error structure and logit-link were used to analyze differences in the proportion of *A. mexicanum* seeds: (1) removed from open and closed plots (exclosures) between sites (flats and slopes, and (2) that germinated in open and closed plots between sites. We corrected for extra-binomial error in both analyses, and evaluated significance of the regression coefficients with a z-test. Differences between regression coefficients were evaluated with Wald’s test.

Multiway contingency tables (MCT; Christensen 1997) were used to analyze; (1) differences in the frequencies of undispersed *A. mexicanum* seeds from the seed-removal plots that germinated across sites and periods; (2) differences between sites in the frequencies of germinated *A. mexicanum* seeds that were either dispersed or undispersed; and (3) differences in fate for threaded seeds among sites and periods, with fate pooled into two categories: eaten (eaten + burrow) and cached (surface + buried). MCTs are used to analyze frequencies when there are more than two categorical response (germinated vs. ungerminated, eaten vs. cached) and predictor variables (dispersed vs. undispersed, site, time period). The significance of the individual and interactive effects of the variables is tested by removing each variable from the model and evaluating the reduction in fit relative to the full model (all variables included in the model). Reduction in model fit is evaluated by the difference in the likelihood-ratio $\chi^2$-value between the full and reduced models (Christensen 1997). Because of small sample sizes, data on dispersed *A. mexicanum* seeds were pooled across time periods.

**Results**

Small mammal abundance and removal of *Heteromys desmarestianus*

Density of *H. desmarestianus* on the flats was 8–10 times greater than that of *Ototylomys phyllois* or *Sigmodon hispidus* (Table 1). In general, density of *H. desmarestianus* was 4.5 times greater on the flats than on the slopes (Table 1). Removal trapping of *H. desmarestianus* between June 2004 and August 2004 resulted in a 90% decrease in their abundance relative to the control grids. Density of *H. desmarestianus* in the DR grids during this period was comparable to or less than its density on the slopes (Table 1).

Density of *O. phyllois* was on average 4.5 times greater on the slopes than on the flats, while density of *S. hispidus* was 4–10 times greater on the flats than the slopes (Table 1). There was a significant decline in captures of *H. desmarestianus* and *S. hispidus* with increasing elevation ($r = -0.915$ and $-0.704$, respectively; Fig. 1). Mean density of *H. desmarestianus* (per hectare) on the flats (excluding the removal period) was $50.3 \pm 1.4$ SE and on the lower slopes $44.0 \pm 4.9$ SE ($t = 1.320$, $df = 4$, $P = 0.257$). Mean density of *H. desmarestianus* on the mid and upper slopes was $8.9 \pm 1.2$ SE, which was significantly lower than their density on the flats ($t = 9.053$, $df = 4$, $P \leq 0.001$). Captures of *O. phyllois* increased significantly with increasing elevation ($r = 0.745$; Fig. 1). Eighty-four percent of the captures of *H. desmarestianus* occurred $\leq 100$ m above the flats. No *S. hispidus* were captured $>120$ m above the flats. Sixty-seven percent of the captures of *O. phyllois* occurred $\geq 100$ m above the flats.

**Distribution and abundance of Astro Caryum mexicanum**

Densities of adult, sapling, and seedling *A. mexicanum* (stems $0.005$ ha$^{-1}$) were significantly lower on the slopes than the flats ($P < 0.0001$; Electronic Appendix A). Seedling density was $14.00 \pm 1.84$ SE on the flats compared to $0.27 \pm 0.07$ SE on the slopes. Sapling density on the flats was $5.53 \pm 0.59$ SE and adult density $6.90 \pm 0.58$ SE. Sapling density on the slopes was $0.15 \pm 0.05$ SE and adult density $1.03 \pm 0.15$ SE. There was an inverse relationship between density of *A. mexicanum* adults and elevation ($r = -0.756$; Fig. 1). Seventy-six percent of *A. mexicanum* adults occurred below $100$ m. Density of *H. desmarestianus* had a strong positive correlation with density of adult *A. mexicanum* (Fig. 2). More than 81% of the variation in mean density of *H. desmarestianus* was explained by variation in density of *A. mexicanum*.

**Seed removal**

**Seed-removal plots**

Removal rates and the total proportion of *A. mexicanum* seeds removed were significantly greater on the flats than the slopes in the three periods when density of *H. desmarestianus* was not manipulated ($P \leq 0.0001$; Fig. 3). The total proportion of *A. mexicanum* seeds removed was $31\%$
Table 1  Density estimates (individuals ha\(^{-1}\) ± SE) of three small mammal species at two sites [benches on the floodplain above the river (Flats), hillsides above the flats (Slopes)] in the Maya Mountains of southern Belize.

| Month/year | Density (individuals ha\(^{-1}\)) |
|------------|----------------------------------|
|            | Slopes | Control | Removal |
| **Heteromys desmarestianus** | | | |
| January 2004 | 25.6 ± 4.0 | 19.9 ± 1.8 | |
| February 2004 | 6.9 ± 0.4 | 36.4 ± 1.1 | 44.7 ± 1.0 |
| March 2004 | 42.8 ± 0.8 | 40.0 ± 1.0 | |
| April 2004 | 43.8 ± 1.1 | 44.4 ± 1.0 | |
| May 2004 | 10.2 ± 0.5 | 45.0 ± 0.8 | |
| June 2004 | 5.0 ± 0.3 | | |
| July 2004 | 5.6 ± 0.3 | | |
| August 2004 | 67.7 ± 2.6 | 5.0 ± 0.1 | |
| September 2004 | 14.5 ± 0.7 | | |
| October 2004 | 58.5 ± 1.2 | 71.0 ± 2.6 | |
| December 2004 | 14.1 ± 0.7 | 48.0 ± 1.0 | 62.1 ± 1.0 |
| March 2005 | 20.1 ± 0.8 | 71.5 ± 1.8 | 82.7 ± 1.3 |

| Month/year | Density |
|------------|--------|
|            | Flats  |
| **Ototylomys phyllotis** | |
| January 2004 | 2.0 ± 0.0 | |
| February 2004 | 3.3 ± 0.0 | 4.0 ± 2.0 |
| March 2004 | 3.5 ± 1.5 | |
| April 2004 | 3.5 ± 1.5 | |
| May 2004 | 7.2 ± 0.4 | |
| June 2004 | | |
| July 2004 | | |
| August 2004 | | 2.0 ± 0.0 |
| September 2004 | 12.8 ± 0.5 | |
| October 2004 | 3.5 ± 1.5 | |
| December 2004 | 15.3 ± 0.6 | 2.1 ± 0.3 |
| March 2005 | 16.3 ± 0.6 | 2.0 ± 0.0 | |

| Month/year | Density |
|------------|--------|
|            | **Sigmodon hispidus** |
| January 2004 | 8.0 ± 1.6 | |
| February 2004 | 1.0 ± 0.1 | 10.3 ± 1.9 |
| March 2004 | 7.1 ± 1.8 | |
| April 2004 | 3.7 ± 0.1 | |
| May 2004 | 0 | |
| June 2004 | | |
| July 2004 | | |
| August 2004 | 3.0 ± 0.9 | |
| September 2004 | 1.4 ± 0.1 | |
| October 2004 | 9.5 ± 2.3 | |
| December 2004 | 1.3 ± 0.1 | 5.1 ± 0.2 |
| March 2005 | 2.0 ± 0.1 | 8.0 ± 1.4 | |

Control (no removal of *H. desmarestianus*) and removal plots (removal of *H. desmarestianus*) were on the Flats.

a Months when density of *H. desmarestianus* was reduced.

greater on the flats than on the slopes. Mean time to removal on the flats ranged from 13 to 31 days, while on the slopes it ranged from 36 to 57 days. Excluding the DR grids from June to August 2004, the total proportion of *A. mexicanum* seeds removed on the flats was 0.93 (±0.03 SE). There was a significant decrease in removal of *A. mexicanum* seeds on the slopes with increasing elevation ($F_{3,104} = 15.43$, $P < 0.0001$). The total proportion of *A. mexicanum* seeds removed on the lower 50 m of the slope was 0.84 (±0.05 SE), compared to 0.57 (±0.05 SE) 51–150 m above the flats, and 0.25 (±0.07 SE) above 150 m.

Reduction in density of *H. desmarestianus* from June to August 2004 resulted in a 70% decrease in the total proportion of *A. mexicanum* seeds that were removed on the flats ($F_{6,6} = 11.69$, $P = 0.0040$; Electronic Appendix B). Removal rates were significantly lower in the DR grids than in the controls or on the slopes during this period ($P < 0.0001$; Fig. 3). Mean time to removal in the control grids was 28 days, whereas it was 143 days in the DR grids and 57 days on the slopes.

Exclosures

No *A. mexicanum* seeds were removed from within the exclosures. Almost all (98.8%) of the *A. mexicanum* seeds were removed from the open plots on the flats, compared to 22.7% on the slopes ($\chi^2 = 8.12$, df = 7, $P < 0.0001$).

Consumption of *A. mexicanum* seeds

A total of 51 photographs (39 on the flats, 12 on the slopes) of *H. desmarestianus* removing *A. mexicanum* seeds were taken. There were no photographs of other small mammals removing seeds. There was no evidence (strings above rather than below ground vegetation, seeds taken up trees) of other mammals taking any *A. mexicanum* seeds.

All *A. mexicanum* seeds offered to *H. desmarestianus* during the feeding trials were eaten within 3 days. *O. phyllotis* and *S. hispidus* consumed none of the *A. mexicanum* seeds.

Seed germination

Seed-removal plots

Overall, 89 of 1,171 (7.3%) undispersed *A. mexicanum* seeds germinated from January 2004 up to and including March 2005 (Table 2). A total of 51 germinated on the slopes and 38 on the flats. There was no significant difference in the percentage that germinated across time periods ($\chi^2 = 8.39$, df = 9, $P = 0.495$) or in the percentage that germinated in the control, DR, and slope grids ($\chi^2 = 9.43$, $P = 0.009$).
Germination rates in the control plots ranged from 0 to 4.2%, from 0 to 10.6% in the removal grids, and from 4.8 to 8.4% on the slopes.

**Threaded seeds**

There was no significant difference in the percentage of dispersed seeds that germinated on the slopes and the flats (7 vs. 4%, respectively; $\chi^2 = 1.22, df = 1, P = 0.269$). However, the total number that germinated on the flats was almost 3 times greater than on the slopes ($n = 17$ vs. $n = 6$, respectively).

There was no significant difference in the percentage of A. mexicanum seeds that germinated across time periods when dispersed and undispersed seed data were combined ($\chi^2 = 7.67, df = 6, P \geq 0.264$). However, dispersed seeds were almost 5 times more likely to germinate than undispersed seeds ($\chi^2 = 42.75, df = 4, P < 0.0001$; Table 2).

**Exclosures**

Germination rates in closed and open plots varied between flats and slopes ($z = 3.407, P = 0.0003$). The germination rate of A. mexicanum seeds in enclosed plots on the slopes was 6.0 (±0.6 SE) while that in open plots on the slopes was 5.0 (±0.8 SE; $\chi^2 = 0.016, df = 1, P = 0.903$). In contrast,
germination rates on the flats were 5 times greater in the enclosed plots (5.2 ± 0.7 SE) than in the open plots (0.7 ± 0.01 SE; \( \chi^2 = 20.722, df = 1, P < 0.0001 \)).

### Seed fate

The fates of 496 threaded \( A. \) mexicanum seeds were determined during the study. Of this total, 65 (13.1%) were cached and the remainder either eaten or taken into a burrow. Excluding the period when the density of \( H. \) desmarestiansus was reduced in the DR grids, the percentage of seeds on the flats that was eaten ranged from 81 to 97%, while the percentage eaten on the slopes ranged from 75 to 94% (\( \chi^2 = 3.34, df = 4, P = 0.504; \) Fig. 4). During the period when density of \( H. \) desmarestiansus was reduced, the proportion of seeds eaten in the DR grids fell to 57% (\( \chi^2 = 14.58, df = 6, P < 0.024; \) Fig. 4).

### Discussion

While many abiotic and biotic factors likely contribute to the regional distributions of \( Heteromys \) desmarestiansus and \( Astrocaryum \) mexicanum, their mutual relationship as seed predator and food resource (Price and Jenkins 1986) clearly has a strong effect on the distribution and abundance patterns of each species in the BNR. \( A. \) mexicanum influences abundance of \( H. \) desmarestiansus through food availability,
while *H. desmarestianus* influences germination rates of *A. mexicanum* seeds, and possibly abundance in later life history stages of the palm, through the interactive effects of seed predation and seed dispersal (Table 3).

Our hypothesis that germination rates of *A. mexicanum* seeds would be more strongly influenced by seed predation and dispersal than abiotic conditions was largely borne out. Many kinds of physical factors are known to influence palm density (Clark et al. 1995; Svenning 1999; Vormisto et al. 2004), and germination rates of *A. mexicanum* seeds would have varied independently of density of *H. desmarestianus* if abiotic conditions, especially those related to differences between slopes and flats (e.g. soil depth, soil texture, soil moisture capacity, nutrients), were a more important influence than biotic interactions. This was not the case though. When protected from removal by *H. desmarestianus*, germination rates of *A. mexicanum* seeds were similar on the flats and slopes. However, densities of *A. mexicanum* seedlings, saplings, and adults were an order of magnitude lower on the slopes than the flats, indicating that seed predation and dispersal were the dominant influences on germination of *A. mexicanum* seeds. This does not imply though that abiotic factors are not important for recruitment, because they may be exerting a strong influence on growth and survival rates of *A. mexicanum* seedlings and saplings.

Our hypothesis that seed predation would have a stronger influence than seed dispersal on germination rates of *A. mexicanum* seeds was not entirely supported. Germination rates on the flats were greater in enclosed than open plots and in the seed-removal plots when abundance of *H. desmarestianus* in the DR grids was reduced, which was consistent with our hypothesis. However, germination rates on the slopes were similar between enclosed and open plots and between the flats and slopes in the seed-removal plots, and the proportions of seeds eaten on the flats and slopes were similar. Critically, the number of seeds that were dispersed was dramatically lower in areas where density of *H. desmarestianus* was low, and dispersed seeds had much greater germination rates than undispersed seeds. This indicates that, in the BNR, the seed stage of *A. mexicanum*'s life history is being strongly influenced by a complex interaction between density of *H. desmarestianus*, seed predation, and seed dispersal.

Low density of *H. desmarestianus* resulted in lower predation rates on *A. mexicanum* seeds, but this does not
Table 3  Summary statistics (mean ± SE) for nine variables related to the interactions between the small mammal seed predator/disperser *H. desmarestianus* and the palm *A. mexicanum* in the BNR, Belize, from January 2004 up to and including April 2005

| Variable                  | Flats       | Slopes          | Removal       |
|---------------------------|-------------|-----------------|---------------|
| *Heteromys* density (ha⁻¹) | 50.3 (1.5)  | 13.2 (0.6)      | 5.2 (0.2)     |
| *Astrocarium* density     | 345.0 (28.9)| 103.3 (14.8)    | 420.1 (44.5)  |
| (mature ha⁻¹)             |             |                 |               |
| *Astrocarium* density     | 276.7 (29.7)| 15 (4.6)        | 176.7 (29.3)  |
| (saplings ha⁻¹)           |             |                 |               |
| *Astrocarium* density     | 700.0 (91.8)| 26.7 (7.1)      | 663.3 (125.3) |
| (seedlings ha⁻¹)          |             |                 |               |
| Seed dispersal rate (%)   | 92.4 (2.0)  | 59.0 (3.7)      | 27.7 (6.8)    |
| Seed predation rate (%)   | 86.6 (2.1)  | 86.3 (4.0)      | 57.1 (3.7)    |
| Germination rate undispersed seeds (%) | 2.4 (1.3) | 7.6 (0.9) | 10.6 (2.2) |
| Germination rate dispersed seeds (%) | 3.9 (0.8) | 7.3 (3.6) |               |
| Total number of seeds germinating | 17 | 6 |               |

Statistics for the flats include control (n = 3) and removal (n = 3) plots on the floodplain exclusive of the period May–July 2004. Statistics for the removal plots are for the period May–July 2004 when trapping was used to reduce density of *H. desmarestianus* by 90%. Statistics for the slopes are for plots (n = 3) located on the hillsides above the floodplain. Empty cells in the removal column indicate that too few tagged seeds were dispersed (n = 7, none germinating) to derive meaningful estimates of germination during this period.

There are indications that the distribution of *A. mexicanum* in the BNR is influenced as much or more by the number than the proportion of seeds that are dispersed. *H. desmarestianus* consumed approximately the same proportion of *A. mexicanum* seeds on the flats as on the slopes, but the number of seeds that were dispersed on the flats was greater than on the slopes. In addition, despite high seed predation on the flats and similar germination rates among the flats and slopes, seedling density of *A. mexicanum* on the flats was considerably higher than on the upper slopes. This suggests a parallel between seed dispersal and predator–prey interactions; in many instances it may be critical to determine if germination depends on the number of seeds that are dispersed or the ratio relative to seed predator abundance (Abrams and Ginzburg 2000).

Mutualisms between plants and seed dispersers in the tropics are generally considered to be highly diffuse and co-evolution rare (Herrera 1985). However, relatively specific facultative mutualisms can develop over more limited time and spatial scales and have a significant influence on distribution and abundance patterns of the species involved in the relationship (Bronstein 1994; Theimer 2005). Hulme (2002) hypothesized that granivores would likely act as mutualists under three conditions: when the plant depends on animals to disperse their seeds, when seeds are scattered rather than larderhoarded, and when resources are scarce. The relationship between *H. desmarestianus* and *A. mexicanum* clearly met two of these three criteria: seeds of *A. mexicanum* are dispersed exclusively by mammals, and while *H. desmarestianus* does larderhoard, scatterhoarding is also quite common. The relationship between caching rates and food availability was less clear. The overall high availability of food throughout most of this study limited the extent we could evaluate this relationship, but it is suggestive that caching rates of *A. mexicanum* in the BNR were twice as high in the year after a hurricane (October 2001) when overall food resources were very low (Klinger and Rejmánek 2009). However, densities of *H. desmarestianus* were also very low during this period (Klinger 2007). The strong relationship between *H. desmarestianus* and *A. mexicanum* in the BNR existed prior to the hurricane (Brewer and Rejmánek 1999), so it is unlikely our observations were artifacts of this major disturbance. The variation in caching rates in the year after the hurricane and when we conducted this study (3 years post-hurricane) raises the possibility though that it is not just resource scarcity but the per capita amount of food available to seed predators/dispersers that influences the formation of mutualisms (Theimer 2005).

The relationship between *H. desmarestianus* and *A. mexicanum* in the BNR would appear to be an example of what are typically considered diffuse interactions between palms and their seed predator/disperser species (Zona and
The seeds of *A. mexicanum* can, potentially, be handled by many other mammal species, and while *H. desmarestianus* consumes a wide variety of seeds (Klinger and Rejmánek 2009) it is clearly the only mammal in the BNR that consumes or disperses *A. mexicanum* seeds to any meaningful degree. Such specificity in a plant-seed disperser relationship is generally thought to be relatively uncommon; plant seeds are typically dispersed by multiple animal species and animals usually consume and disperse seeds of many plants (Wheelwright and Orians 1982). But plant–seed disperser relationships that are evolutionarily diffuse may still be specific enough at smaller spatial and temporal scales to have significant effects on density and distribution of both the plant and disperser species.

Reducing density of *H. desmarestianus* allowed a direct evaluation of the degree to which their seed dispersal benefited *A. mexicanum*. Reducing density of *A. mexicanum* seeds would have allowed a direct evaluation of the degree to which they benefited *H. desmarestianus*, but this was logistically impractical to do. However, there is abundant evidence of the importance of this part of the mutualism. Population dynamics and demography of mammals in the tropics are often related to bottom-up effects (Adler and Beatty 1997; Klinger 2006, 2007), and *A. mexicanum* seeds are clearly a very important food resource for *H. desmarestianus*. Survival rates of subadult *H. desmarestianus* are positively related to abundance of *A. mexicanum* seeds (Klinger 2007), and density of *H. desmarestianus* is greater in areas with greater abundance of *A. mexicanum* seeds. Because it is their only year-round food source and influences transition rates of subadults to adults, availability of *A. mexicanum* seeds likely sets a lower threshold of density for *H. desmarestianus*. This explains in large part why density of *H. desmarestianus* was lower on the slopes than the flats. Moreover, generally it suggests that when seed disperser mutualisms are tightly coupled then the interaction may act as a feedback system determining distribution and abundance of each species. Studies of mutualisms in other systems have often focused on one pathway in the interaction while assuming that the pathway in the opposite direction was also important (Longland et al. 2001). Even though these assumptions may be correct, simply assuming does not allow an evaluation of how strong the mutualism truly is.

Logistic constraints (trap availability, topography, and time) required us to have lower densities of traps and seed plots on the slopes than on the flats. However, differences in trap and seed plot densities likely had small or negligible effects on density estimates and seed-removal rates because their influence was minimal relative to home range size and density of *H. desmarestianus*. The minimum home range size for *H. desmarestianus* is approximately 100 m² (Fleming 1974), and their density and seed-removal rates on the lower slopes were comparable to those on the flats.

Because our study was restricted to the BNR our inferences must be limited to this particular forest. The densities of *H. desmarestianus* and *A. mexicanum* in the BNR are very similar to those reported from other forests in the northern Neotropics (Martinez-Ramos 1997; Martinez-Gallardo and Sanchez-Cordero 1997), but the reserve differs in some important respects from many other forests in Central America. The BNR has a high level of protection and is surrounded by a national park, a wildlife sanctuary, and several forest reserves. Consequently, illegal activities have been relatively localized and largely near the boundaries of the reserve. This is in contrast to many other protected areas in the Neotropics, which frequently exist as habitat islands with high levels of illegal activities, altered forest structure, and a depauperate fauna (Dirzo and Garcia 1992; Wright et al. 2000). Differences in species composition of the fauna and flora in these forests, either because of natural or anthropogenic factors, could result in very different interactions than we observed in the BNR. Despite this, we suspect that strong local plant-seed disperser mutualisms are more common than thought (Gove et al. 2007). However, we also expect that these mutualisms are restricted spatially and do not persist for long periods of time. Interaction strengths and direction may shift, and possibly quite rapidly, due to changing environmental conditions (Ovadia and Schmitz 2004) or anthropogenic influences (Wright et al. 2007). Nevertheless, even though they may be relatively localized both spatially and temporally, these conditional mutualisms likely leave a disproportionately strong historic imprint on the population structure and distribution of long-lived plant species.

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