LETTER

Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm

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Abstract

Negative density dependence (NDD) of recruitment is pervasive in tropical tree species. We tested the hypotheses that seed dispersal is NDD, due to intraspecific competition for dispersers, and that this contributes to NDD of recruitment. We compared dispersal in the palm *Attalea butyracea* across a wide range of population density on Barro Colorado Island in Panama and assessed its consequences for seed distributions. We found that frugivore visitation, seed removal and dispersal distance all declined with population density of *A. butyracea*, demonstrating NDD of seed dispersal due to competition for dispersers. Furthermore, as population density increased, the distances of seeds from the nearest adult decreased, conspecific seed crowding increased and seedling recruitment success decreased, all patterns expected under poorer dispersal. Unexpectedly, however, our analyses showed that NDD of dispersal did not contribute substantially to these changes in the quality of the seed distribution; patterns with population density were dominated by effects due solely to increasing adult and seed density.

Keywords

Clumping, competition for dispersers, escape, intraspecific competition, Janzen-Connell, population regulation, recruitment limitation, seed limitation, species coexistence, tropical forest.

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INTRODUCTION

Conspecific neighbours often have more negative effects on individual plant performance (e.g. survival, growth and recruitment) than do heterospecific neighbours, a phenomenon known as negative density dependence (NDD). NDD constitutes a strong stabilising force for population regulation and species coexistence (Chesson 2000). Many studies have found NDD of plant performance in diverse tropical forests (Wright 2002). NDD can arise because attacks by natural enemies increase disproportionately with local conspecific density (Janzen 1970; Connell 1971), and/or because competition for resources is more intense between conspecifics than heterospecifics (e.g. Tilman *et al.* 1996). In tropical forests, NDD is generally attributed to natural enemies (Hammond & Brown 1998; Terborgh 2012). However, it is also possible that NDD results, at least in part, from intraspecific competition for seed dispersers.

Seed dispersers as a limiting resource

Seed dispersal is critical for colonising vacant sites, escaping natural enemies concentrated around parents and reducing kin competition, (Nathan & Muller-Landau 2000). Vertebrates are agents of seed dispersal for 70–100% of tropical tree species (Willson *et al.* 1989), and may thus be a key limiting

resource for the majority of tree species in most tropical forests (Howe & Estabrook 1977; Manasse & Howe 1983). Because disperser populations are limited by food availability during the season of greatest food scarcity (Leigh 1999), they are easily satiated in times of greater food availability, setting the stage for competition for dispersers (e.g. Wheelwright 1985; Hampe 2008).

Plant species vary widely in the timing of fruit production and the composition of their disperser coteries. Thus, they should compete for dispersers more strongly with conspecifics, which have exactly the same disperser coteries and fruiting phenologies, than with heterospecifics (Howe & Estabrook 1977). Therefore, intraspecific competition for dispersers should increase with a tree species' abundance (Hampe 2008), and the rate at which fruits are consumed, and seeds removed and dispersed should decline, as should the dispersal distance.

Empirical studies have shown that seed removal indeed depends positively on disperser abundance (e.g. Alcántara *et al.* 1997), and negatively on seed abundance (e.g. Jansen *et al.* 2004) and tree density (e.g. Manasse & Howe 1983; Beck & Terborgh 2002). This indicates that intraspecific competition for dispersers – sometimes referred to as disperser satiation – exists and can indeed lead to NDD of seed removal. Intraspecific competition can also reduce dispersal distance in years of higher seed abundance (Vander Wall 2002; Jansen *et al.* 2004) and in areas with higher fruit

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availability (Gálvez *et al.* 2009; Klinger & Rejmánek 2009; Morales *et al.* 2012). To date, however, no study has evaluated whether competition for an entire community of seed dispersers can cause NDD of dispersal, and whether and how this contributes to NDD of recruitment.

Consequences for recruitment

NDD of seed dispersal may translate to population-level NDD of recruitment because dispersal promotes recruitment in at least three fundamentally different ways. First, dispersal reduces seed limitation, i.e. the failure of trees to establish recruits at potentially favourable sites because no seeds or insufficient seeds arrive there (Nathan & Muller-Landau 2000; Schupp *et al.* 2002). Shorter dispersal implies that, all else equal, the available seeds end up in fewer sites. Second, dispersal allows offspring to escape the vicinity of the parent, a conspecific adult. Many studies have shown that offspring mortality rates are higher near conspecific adults (reviewed in Hammond & Brown 1998; Wright 2002), a pattern most often attributed to so-called distance-responsive natural enemies associated with adults (Janzen 1970; Connell 1971), such as host-specialised pathogens and arthropods (e.g. Augspurger & Kelly 1984; Alvarez-Loayza & Terborgh 2011). Shorter dispersal implies that more seeds end up near their parent. Finally, dispersal can decrease the spatial aggregation (clumping or crowding) of offspring by spreading seeds over a larger area. Establishment success and subsequent survival decreases with local conspecific seed density (e.g. (Harms *et al.* 2000; Comita *et al.* 2010; Bagchi *et al.* 2014), a pattern generally attributed to density-responsive natural enemies (sensu Janzen 1970) such as host-specialised pathogens and arthropods (e.g. Augspurger & Kelly 1984; Bell *et al.* 2006; Bagchi *et al.* 2014). Shorter dispersal implies that seeds, on average, experience higher local seed density.

Despite these important functions of dispersal, it is not evident that NDD of dispersal will translate to NDD of recruitment. Dispersal is inherently less likely to result in escape from conspecifics as density of conspecific adults and offspring increases. For example, increased dispersal limitation in dense populations will to some degree be offset by reduced source limitation because so many more seeds will be available to colonise sites. Also, even if seed dispersal is identical, the mean distance of dispersed seeds to the nearest adult will still decline with density because, on average, there is an adult closer to every point. The essential question is whether NDD dispersal causes seed limitation, distance-to-adult and crowding to change faster or slower (in the case of seed limitation) than they would as passive consequences of changes in adult density.

This study

We tested the hypotheses that (1) competition for seed dispersers increases with population density, depressing seed removal rates and dispersal distances, and that (2) reduced seed dispersal at higher population density significantly increases seed limitation, proximity to adults and crowding beyond the changes due solely to increasing adult and seed density. Our approach was to compare seed dispersal of the vertebrate-dispersed palm species *Attalea butyracea* among areas on Barro Colorado Island (BCI), Panama that ranged widely in adult density. We found that intraspecific competition for dispersers indeed caused NDD of seed dispersal. Unexpectedly, however, this did not affect NDD of seedling recruitment beyond effects solely due to increasing adult density.

METHODS

Study site and species

Fieldwork was conducted in old secondary moist tropical forest (90–130 years old) on the south-eastern half of BCI (9°9′ N, 79°51′ W), a 1560-ha island located in the Gatun Lake section of the Panama Canal (Leigh 1999).

Attalea butyracea (Mutis ex L.f.) Wess. Boer (henceforth *Attalea*) is a monoecious palm abundant in Central Panama (Wright 1990). Adults can reach heights of ~30 m (De Steven *et al.* 1987). They produce 1-3 pendulous infructescences annually, each containing 100–600 fruits of 3–5 cm. Fruits consist of a hard exocarp enclosing a sweet fleshy mesocarp and a stone (henceforth 'seed'), a hard endocarp that usually contains one seed. Endocarps persist on or in the soil for several years before decomposing (Wright 1983, 1990). Fruits are consumed by many mammal species (Wright & Duber 2001 and references therein), but only Baird's tapir *Tapirus bairdii* ingests the seeds.

On BCI, seed dispersal of *Attalea* is primarily by two rodent species – the Central American agouti (*Dasyprocta punctata*) and the Red-tailed squirrel (*Sciurus granatensis*) – that carry seeds away in their mouth, one at a time, to scatter hoard (Forget *et al.* 1994; Wright & Duber 2001). Reciprocal theft and recaching of seeds can produce stepwise dispersal over distances >100 m (Hirsch *et al.* 2012a; Jansen *et al.* 2012). Agoutis and squirrels, along with the Central American spiny rat (*Proechimys semispinosus*), are the only vertebrates reported to eat *Attalea* seeds on BCI (Forget *et al.* 1994). Two insect seed predators, the bruchid beetles *Speciomerus giganteus* (Chevrolat) and *Pachymerus cardo* (Fahraeus), also attack *Attalea* seeds (Wright 1983).

Forest plots

We used two sets of plots varying in adult *Attalea* density, all located in the same area of old secondary forest (Fig. S1). Seed removal rates and initial seed dispersal distances were quantified in six square 1-ha experimental plots established in 2005, with adult density ranging over 5–29 individuals ha^{-1}. Frugivore visitation, ultimate seed dispersal distance and seedling recruitment were quantified in ten square 4-ha plots established in 2008, with adult densities ranging over 1–25 individuals ha^{-1} (see Visser *et al.* 2011). Plot centres were separated by at least 300 m (Fig. S1). In each plot, we mapped every palm with a bole height >1.3 m, and determined its reproductive status by the presence of infructescences and inflorescences. In the 4-ha plots, we also recorded bole height, a potential predictor of fecundity.

Tree visitation by dispersers

Tree visitation by seed dispersers was estimated by deploying camera traps with passive infrared motion sensors (RC55, Reconyx, Inc. Holmen, WI, USA) below 1–3 fruiting *Attalea* in each of nine 4-ha plots during July–August 2009 (21 palms in total; the tenth plot had no suitable fruiting *Attalea* during the study period). Cameras were placed ca. 20 cm above the ground 3–4 m away from the focal palm facing the fallen fruits. Deployment duration averaged 8.4 days per tree, and 19.6 days per plot. We analysed the photographs and identified all mammal to species (Kays *et al.* 2011). For each species, visitation rate was calculated as the number of visits (separated by >3 min) divided by deployment duration.

Seed removal and initial dispersal distance

Seed removal rates and initial dispersal distances were measured in the six 1-ha plots during August–September 2005. To quantify seed removal, we placed three sets of 15 seeds – a mix of seeds with and without fruit flesh – below the crowns of three fruiting *Attalea* in each plot (135 seeds per plot), and recorded how many remained after 1, 2, 4, 8, 16, 32, 64 and 128 days. We calculated time to removal, the complement of removal rate, as the geometric mean of the days until the census at which the seed was no longer present. Initial seed dispersal distance was quantified by tracking thread-tagged seeds (Forget & Wenny 2005). A 70-cm thread with 10 cm of pink flagging tape with a unique number written on it was attached to the seed via a tiny hole drilled though the woody tip of the endocarp. Thread tags enable retrieval of seeds after removal even if the seed is buried, as the pink flagging remains above ground. We placed five sets of five tagged, de-fleshed seeds at the base of three fruiting individuals in each plot (75 seeds per plot), relocated all seeds 7 days after placement by searching the surrounding area for thread marks, measured the distance from the original location, fitted a log-normal distribution to the Kaplan–Meier function of distance (after Jansen *et al.* 2004; Hirsch *et al.* 2012b) and extracted the median distance.

Ultimate seed dispersal distance

Ultimate dispersal distances can be much larger than initial distances, due to reciprocal theft and recaching of seeds by rodents (Jansen *et al.* 2012). We used inverse modelling (IM) to estimate ultimate dispersal distance from the post-dispersal spatial distribution of empty and filled endocarps in the ten 4-ha plots. We sampled 33 1 × 1 m quadrats within the central 100 × 100 m of each plot during January–August 2008 (see Visser *et al.* 2011). Two quadrats were placed at computer-generated random locations in each of the 16 subplots of 25 × 25 m, a 33rd quadrat was placed randomly beneath the central palm. The surface and top 5 cm of soil of each quadrat were thoroughly searched for endocarps using a small rake. We excluded fresh endocarps from the early fruiting season of 2008, as well as endocarps so old they could be crushed by hand, hence the endocarps we counted represent those produced during the fruiting seasons of 2007, 2006 and probably 2005.

We used standard IM methods (Ribbens *et al.* 1994; Muller-Landau *et al.* 2008) to model the seed shadow of an individual tree as the product of its estimated seed production and its dispersal kernel, the two-dimensional probability distribution of seed displacement. The expected number of endocarps at each quadrat was the sum of expected contributions of all adults on the plot, and from adults outside the plot under the assumption that endocarp production per unit area off-plot equalled that on the plot (Muller-Landau *et al.* 2008). Observed endocarp numbers were assumed to follow a negative binomial distribution around expected values (Clark *et al.* 1999).

To test for the influence of palm density on seed dispersal distances, we first separately fitted endocarp dispersal kernels for each plot, and second fitted an overall model in which dispersal parameters varied with adult density among plots. We combined three fecundity models (constant, linear increase with height, asymptotic increase with height) with seven dispersal kernels (Erlang, 1- and 2-parameter 2Dt, 1- and 2-parameter Weibull and 1- and 2-parameter lognormal; see Table S1) (Ribbens *et al.* 1994; Clark *et al.* 1999; Klein *et al.* 2006; Jongejans *et al.* 2008). In the overall model, the scale parameter of the dispersal kernels was allowed to vary among plots as a function of adult density (Table S1). We tested linear and exponential dependence on adult density against a constant model (no dependence). For each model, we searched for the maximum likelihood parameter estimates using the Nelder–Mead downhill simplex method (Nelder and Mead 1965). We used Akaike's information criterion (AIC) for model selection, and calculated median dispersal distances for the best-fitting model.

Seedling recruitment

To assess recruitment success, we mapped all *Attalea* seedlings across 2500 m² in each of the ten 4-ha plots during January–March 2008. We subdivided the central ha of each plot into 16 subplots of 25 × 25 m, and randomly selected one of the four inner subplots and three of the 12 outer subplots. We mapped all offspring in those subplots and tagged them with numbered vinyl loop tags. Seedlings were defined as individuals that had simple leaves only (as opposed to compound leaves). We calculated the ratio of seeds to seedlings and seedlings to adults based on their densities.

Consequences for recruitment

To assess the consequences of dispersal, we calculated three measures of seed distribution relevant for recruitment success from simulations parameterised with fitted seed dispersal models. (1) Seed limitation was quantified as its complement; the proportion of 1-m² quadrats reached by at least one seed. (2) Seed escape from adults was quantified as the mean distance of dispersed seeds to the nearest conspecific adult trunk in the mapped plot. (3) Seed crowding was quantified as the mean over all seeds of the number of conspecific seeds in the same 1-m² sample.

To determine whether trends in these three measures among plots reflected declines in seed dispersal quality beyond effects

solely due to adult density itself, we compared values of these metrics obtained in simulations using each plot's empirically fitted dispersal kernel ('observed dispersal') with two sets of simulations that applied the same dispersal kernel in all plots: 'Good dispersal' simulations used the kernel of the plot with the lowest population density (and most extensive dispersal), whereas 'poor dispersal' used the kernel of the plot with the highest population density (and least extensive dispersal). For all simulations, seed production was set to 4247 seeds per adult (the fitted value in the hierarchical model).

Statistical analyses

We used linear models to quantify among plot relationships of adult density with frugivore visitation, time to seed removal, initial seed dispersal distance and ultimate dispersal distance. NDD of seed dispersal would be evident if the slopes of the log–log relationships with adult density were significantly greater than zero for time to removal, and were significantly less than zero for the other three metrics. Seed removal rates were additionally evaluated using a Cox proportional hazards model of time-to-removal. The relationship of ultimate dispersal distance to adult density was evaluated by comparing the fits of hierarchical models that assumed constant dispersal distances across all 10 plots with a model that had dispersal distance vary linearly or exponentially with adult density among plots.

We also used linear models to quantify the relationship between adult density and the three measures of seed distribution for each of the three types of simulation. To meet model assumptions, adult density, distance-to-adult and crowding were $\log_{10}$ transformed, and the proportion of sites with seeds was logit transformed. To distinguish effects of NDD of seed dispersal from effects of adult density alone, we compared the slopes between the relationship for observed dispersal and the relationship for good dispersal (i.e. density-independent

dispersal), using analysis of covariance (ANCOVA). A significantly different slope was interpreted as evidence of NDD of seed dispersal. We assessed how dispersal quality affected seed distributions across the gradient of adult density by comparing the intercepts and slopes of the fitted relationships with adult density between good and poor dispersal. All analyses were conducted in R 3.02 (R Development Core Team 2013).
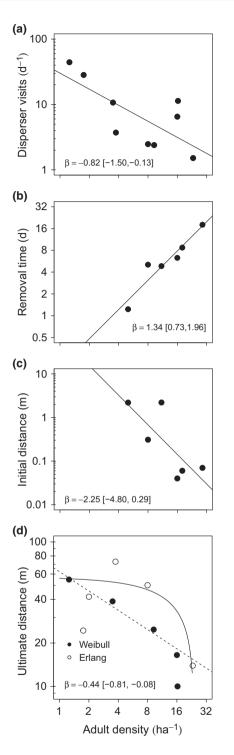
RESULTS

Density dependence of seed dispersal

The camera traps recorded a total of 2076 visits by 15 mammal species, with an average of 11.7 visits day^{-1} (Table 1). Ten frugivorous species were photographed handling (i.e. holding in their paws and/or mouth) a total of 2201 *Attalea* fruits (Table 1). Seeds were removed by agoutis and squirrels (all 21 trees) and tapirs (2 trees). Rates of tree visitation by frugivores ranged 40-fold among the nine plots for both agoutis (1.1–41.6 day^{-1}) and squirrels (0.08–3.4 day^{-1}). Visitation rates by agoutis and squirrels combined decreased significantly with tree density across the ten 4-ha plots (Fig. 1a; log–log regression: $F_{1,7} = 7.9$, $R^2 = 0.53$, $P = 0.026$). The slope of this relationship was significantly smaller than zero ($\beta = -0.82$, $t_7 = 2.8$, $P = 0.013$), indicating that visitation was NDD.

The seed removal rate differed strongly among the six 1-ha plots. The time elapsed until all seeds were removed ranged from 8 to 128 days. Time-to-removal increased with tree density (Fig. 1b; $R^2 = 0.90$, $F_{1,4} = 37.0$, $P = 0.004$). The slope of this relationship was significantly larger than zero ($\beta = 1.34$, $t_4 = 6.08$, $P = 0.002$), indicating that seed removal was NDD. Survival analysis of time-to-removal yielded a similar relationship (Cox regression: $e^{\beta} = 0.09$, Wald$_1 = 18.19$, $P < 0.001$).

Initial dispersal distance – the distances at which we found tagged seeds 7 days after placement – ranged from 0 to

Table 1 Visitation of *Attalea butyracea* palms by mammals on Barro Colorado Island, recorded with camera traps deployed below fruiting individuals.

Species	No. of plots	No. of visits		Visit duration (min)		Fruits handled	
		Total	Rate (day^{-1})	Total	Rate (min day^{-1})	Total	Dispersal
Frugivores							
Central American agouti (*Dasyprocta punctata*)	9	1097	6.21	824	4.66	561	Y
Red-tailed squirrel (*Sciurus granatensis*)	9	293	1.66	112	0.63	150	Y
Collared peccary (*Tayassu tajacu*)	8	272	1.54	1189	6.73	634	N
White-nosed coati (*Nasua narica*)	8	232	1.31	1692	9.57	700	N
Paca (*Agouti paca*)	9	38	0.21	14	0.08	19	N
Common opossum (*Didelphis marsupialis*)	5	24	0.14	44	0.25	22	N
Tome's spiny rat (*Proechimys semispinosus*)	5	22	0.12	3	0.02	3	Y
White-faced monkey (*Cebus capucinus*)	5	10	0.06	2	0.01	8	N
Baird's tapir (*Tapirus bairdii*)	3	9	0.05	132	0.75	103	Y
Mouse spec.	4	9	0.05	0.5	0.00	0	N
Robinson's mouse opossum (*Marmosa robinsoni*)	3	7	0.04	5	0.03	1	N
Non-frugivores							
Northern tamandua (*Tamandua mexicana*)	5	42	0.24	79	0.45	0	N
Red-brocket deer (*Mazama americana*)	8	13	0.07	2	0.01	0	N
Nine-banded armadillo (*Dasypus novemcinctus*)	3	7	0.04	8	0.05	0	N
Tayra (*Eira barbara*)	1	1	0.01	0	0.00	0	N
Total		2076	11.75	4109	23.25	2201	

Figure 1 Seed dispersal in the palm *Attalea butyracea* on Barro Colorado Island for populations with widely ranging adult density. (a) Rates of fruiting-tree visitation by the two principal seed dispersers. (b) Geometric mean time elapsed until seed removal by dispersers (the complement of removal rate). (c) Median seed dispersal distance from the source after 32 days. (d) Median ultimate dispersal distance estimated by hierarchical inverse modelling over all plots simultaneously (solid line), and – for illustration – by inverse modelling for plots individually (dots and dashed line; symbols vary by the function that gave the best model fit). Dots correspond to ten 4-ha (a and d) or six 1-ha (b and c) forest plots. All relationships (lines) imply negative density dependence of seed dispersal.

38.4 m among seeds. Median distances ranged from 0.04 to 2.21 m among the six 1-ha plots, and decreased with adult density (Fig. 1c; log–log regression: $R^2 = 0.60$, $F_{1,4} = 6.0$, $P = 0.07$). The slope of this relationship was significantly smaller than zero ($\beta = -2.25$, $t_4 = 2.46$, $P = 0.035$), indicating that initial dispersal distance was NDD.

We excavated a total of 2272 endocarps across 330 1-m^2 quadrats. Ultimate seed dispersal distance, estimated with IM from the distributions of these endocarps with respect to adult trees, declined with adult density. The dispersal kernels that best fitted the observed distribution patterns for individual plots were the Erlang and the Weibull, each in five of the ten 4-ha plots. Median dispersal distances calculated from these best-fitting dispersal models were negatively related to the density of *Attalea* adults (straight dashed line in Fig. 1d; $R^2 = 0.50$, $F_{1,8} = 7.9$, $P = 0.023$). The slope of this log–log relationship was again significantly smaller than zero ($\beta = -0.44$, $t_8 = -2.81$, $P = 0.011$). The best-fitting dispersal kernel fitted over all plots simultaneously, with hierarchical inverse modelling, was a 1-parameter 2Dt function with the shape parameter fixed at 2 and the scale parameter a fitted as a linear function of palm density D: $a = 7878 - 326 D$ (Fig. S2). The median dispersal distance extracted from this model showed a sharp decline with adult density (curve in Fig. 1d). These results indicate that ultimate dispersal distance was NDD.

Consequences for recruitment

Average seed density ranged over 1.6 orders of magnitude across the ten 4-ha plots, from 0.8 to 31 m^{-2}, and increased significantly with adult density (Fig. 2a; $R^2 = 0.88$, $P < 0.001$). The slope of this relationship did not differ significantly from one ($\beta = 1.23$, $t_8 = 1.44$, $P = 0.09$), implying that seed density was proportional to adult abundance. Seedling density ranged over 1.1 orders of magnitude across the 10 plots, from 0.0124 to 0.142 m^{-2}, and also increased with adult density (Fig. 2a; $R^2 = 0.70$, $P = 0.003$), but much less than proportionally ($\beta = 0.56$, $t_8 = 3.45$, $P = 0.004$). Thus, the ratio of seedlings to seeds declined with population density (Fig. 2b; $R^2 = 0.58$, $F_{1,8} = 11.0$, $P = 0.011$), indicating NDD of seedling recruitment.

To determine to what degree NDD of seedling recruitment was a consequence of NDD of seed dispersal, beyond effects of adult density alone, we explored the effects of seed dispersal and adult density on seed distributions (Fig. 3). Plots with high adult population density had much greater spatial variation in seed density across soil samples than did plots with low adult population density (compare Fig. 3d and h with a and e). Comparison between simulations with fitted kernels for the worst and the best dispersal suggested that dispersal quality had a strong effect on seed distribution (compare Fig. 3c and g with d and h for illustration).

Seed limitation, however, was not significantly affected by NDD of dispersal. The proportion of sites reached by at least one seed – the complement of seed limitation – increased sharply with adult density (Fig. 4a; logit-log regression: $\beta = 2.77$, $F_{1,8} = 315$, $P < 0.001$, $R^2 = 0.98$). In fact, most of the sampling quadrats in dense plots received multiple seeds despite
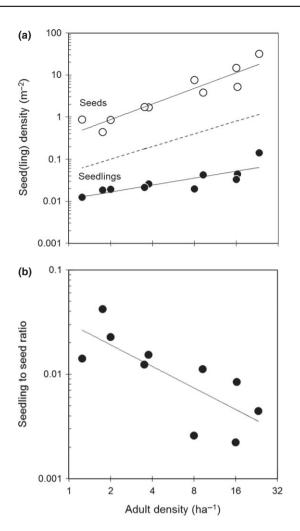
Figure 2 Seedling recruitment success in the palm *Attalea butyracea* on Barro Colorado Island, Panama, for 10 populations with widely ranging adult density. Log–log relationships with adult density of (a) the density of seeds and young (simple-leaved) seedlings and (b) the ratio of seedlings to seeds. Isometric scaling (i.e. proportional recruitment; dashed lines) is shown for comparison. The relationships are significant and imply negative density dependence of seedling recruitment.

the strong decline of dispersal distance with population density (Fig. S3). NDD of seed dispersal did not reduce this increase, as the slope of the relationship did not differ significantly between simulated observed and simulated density-independent dispersal (ANCOVA: $F_{1,17} = 2.28$, $P = 0.14$). Over the gradient of 1–23 adults ha^{-1}, adult abundance increased the odds $\left(\frac{p}{1-p}\right)$ of seed arrival 32-fold, while NDD of dispersal decreased the odds by just 1.3-fold (Fig 4a). Thus, reducing the extent of seed dispersal reduced the proportion of sites reached at low adult densities, but its effects at high population density were overwhelmed by direct consequences of high source availability.

Seed escape from adults within the populations was not significantly affected by NDD either. The mean distance of dispersed seeds to the nearest adult palm declined sharply with adult density (Fig 4b; log–log regression: $\beta = -0.53$, $F_{1,8} - 77$, $P < 0.001$, $R^2 = 0.91$). This decline resulted from adult density itself, as the slope of distance-to-adult did not differ between

simulated observed and simulated density-independent dispersal (ANCOVA: $F_{1,17} = 0.35$, $P = 0.56$). Where adult abundance decreased the distance 4.7-fold, NDD of dispersal decreased it only a further 1.09-fold (Fig 4b). The extent of seed dispersal affected distance-to-adult strongly in plots with low densities but again not at high adult densities. In dense populations, adult trees were so common that dispersed seeds tended to land near one regardless of dispersal quality. Thus, negative consequences of NDD seed dispersal for seed escape from adults were overwhelmed by direct consequences of high adult densities.

Seed crowding, finally, was also not significantly affected by NDD of dispersal. The average neighbourhood seed density experienced by seeds – a measure of seed crowding – increased as a power function of adult density (Fig. 4c; log–log regression: $\beta = 1.22$, $F_{1,8} = 338$, $P < 0.001$, $R^2 = 0.98$). Again, this increase resulted largely from adult density itself, as the slope of the relationship did not differ significantly between simulated observed and density-independent dispersal (ANCOVA: $F_{1,17} = 3.17$, $P = 0.09$). Where adult density increased perceived seed density 32-fold, NDD of dispersal increased it only a further 1.3-fold (Fig 4c). Crowding increased only marginally faster under poor dispersal than under good dispersal. Thus, plots with high adult density already had high seed densities because of the large number of seeds in these systems, and NDD of seed dispersal did not increase crowding further.
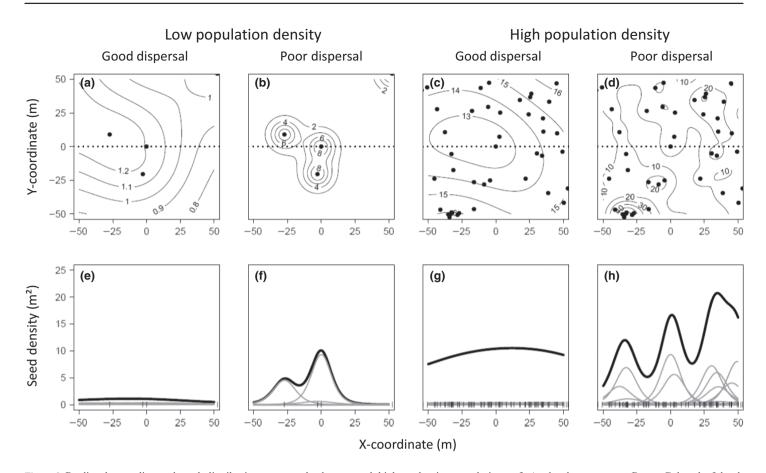
DISCUSSION

We tested the hypotheses that seed dispersal, a key component of reproductive success in seed plants, is NDD due to intraspecific competition for seed dispersers, and that NDD dispersal contributes to NDD of recruitment, a widely observed phenomenon hypothesised to be important to species coexistence in diverse tropical forests (Wright 2002). We found that competition for dispersers indeed caused NDD of seed dispersal. Tree visitation by dispersers, seed removal rate, initial seed dispersal distance and ultimate seed dispersal distance all decreased with increasing population density. We also found evidence for NDD of seedling recruitment. However, NDD of recruitment was not driven by NDD of seed dispersal, as the negative effects on declining dispersal quality were entirely overwhelmed by effects of increased adult and seed abundance alone.

Density dependence of seed dispersal

Our field observations suggest that the NDD of dispersal observed in this study was a consequence of intraspecific competition for seed dispersers. The declines of removal and dispersal with tree population density all indicate that dispersers became increasingly satiated by the combined fruit crops. The concordance of the patterns for different measures of seed removal and dispersal, which reflect data taken over multiple years, strongly suggests that this is a general pattern for our focal species. Our study is the first to show that intraspecific competition for an entire community of seed dispersers (Table 1) can cause NDD of seed dispersal.

Our results are consistent with previous studies that have found negatively density-dependent seed removal and/or

Low population density
Good dispersal
Poor dispersal

High population density
Good dispersal
Poor dispersal

Figure 3 Predicted post-dispersal seed distributions across the lowest and highest density populations of *Attalea butyracea* on Barro Colorado Island, Panama, modelled with the longest and shortest dispersal kernels fitted in this study. (a–d) Actual distributions of adult trees (black dots) with modelled distributions of seeds (density isoclines) over 1 ha. Each plot has one palm in its center. (e–h) Model-estimated seed density along a 100-m cross section of the plots (dotted lines in a–d) for individual trees (grey lines) and the entire population (bold lines). The patterns in a and e resemble the observed seed distributions for low-density populations, and those in d and h resemble the observed seed distributions for high-density populations. The other four panels show hypothetical distributions. The graphs show how reducing dispersal quality leads to more heterogeneous, clumped seed distributions.
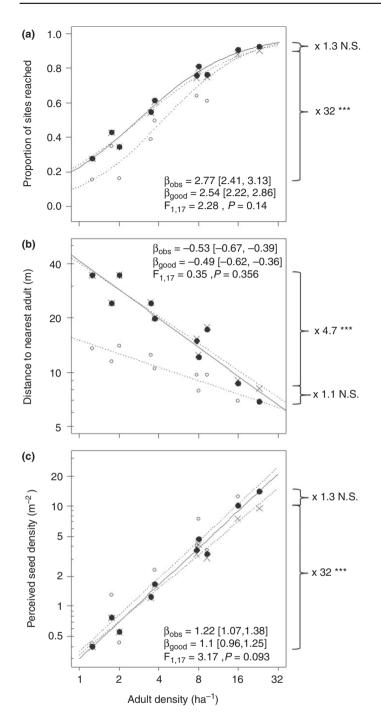
dispersal by scatter-hoarding rodents, marsupials and birds. Scatter-hoarding rodents invest less effort in caching seeds when and where seeds are more abundant, resulting in reduced dispersal distances and reduced rates of recaching (e.g. Vander Wall 2002; Jansen *et al.* 2012). In tropical forests, seed removal and dispersal by scatter-hoarding rodents were reduced in areas with aggregations of adults for *Astrocaryum murumuru* in Peru (Beck & Terborgh 2002) and for *A. standleyanum* in Panama (Gálvez *et al.* 2009). Intraspecific competition for seed dispersers has also been documented for one marsupial-dispersed and several bird-dispersed tropical plant species (Howe & Estabrook 1977; Howe & Vande Kerckhove 1981; Manasse & Howe 1983; Sargent 1990; Poulin *et al.* 1999; Saracco *et al.* 2005; Morales *et al.* 2012).

NDD of dispersal is a particular manifestation of the broader phenomenon of context-dependent dispersal. In general, the per-fruit odds of seed removal and dispersal decline in areas and times where food is so common relative to disperser densities as to result in satiation (e.g. Vander Wall 2002; Jansen *et al.* 2004; Klinger & Rejmánek 2009). One might then expect that dispersal NDD will be ubiquitous, as higher local focal species abundances lead to higher fruit and seed abundances, and thus increased potential for satiation, all else equal. However, multiple factors influence

whether dispersal NDD actually emerges in a particular system, year and site, including especially spatial covariation in abundances of dispersers and of their alternative foods with the abundances of the focal plant species (Klinger & Rejmánek 2009). For example, dispersal NDD need not emerge if focal species fruits or seeds are sufficiently valued and scarce relative to disperser abundance that they are all removed everywhere, or if disperser abundances are able to track spatial variation in focal species fruit or seed availability. We hypothesise that such conditions are the exception rather than the rule, and that dispersal NDD is a common phenomenon among animal-dispersed plants in general.

Consequences for recruitment

We found NDD of seedling recruitment at the population level, consistent with earlier studies (reviewed in Wright 2002). No previous studies identified the causes of such NDD. We had hypothesised that NDD of seed dispersal translates to NDD of recruitment, but found that NDD of seed dispersal in fact had little effect on seed limitation, seed proximity to adults, or seed crowding, the three aspects of seed distributions that we examined.

Figure 4 Effects of NDD seed dispersal on (a) seed limitation, (b) seed escape from adults and (c) seed crowding in the palm *Attalea butyracea* on Barro Colorado Island, Panama, for 10 populations that varied widely in adult density. Plotted values are predictions modelled with the observed dispersal kernels for each plot (filled points and solid line), and – for comparison – with the longest dispersal kernels (crosses and dotted lines) and shortest dispersal kernels (open points and dotted lines) fitted in this study. Panels show (a) the proportion of sites reached by at least one seed (the complement of seed limitation), (b) the average distance of dispersed seeds to the nearest adult, and (c) the density of conspecific seeds perceived by dispersed seeds. The brackets to the right indicate the variation due to adult density (larger numbers) and to NDD of seed dispersal (smaller numbers) for each dependent variable. See text for further explanation.

First, NDD of seed dispersal evidently increased dispersal limitation, a key component of recruitment limitation (Nathan & Muller-Landau 2000), yet this was more than offset by a concomitant reduction of source limitation, resulting from elevated seed availability and wider scattering of seed sources over space. Thus, essentially all sites in dense populations were reached by seeds regardless of dispersal quality. Second, seed proximity to adults increased with adult density, but this was more a consequence of adults being omnipresent in these plots than of seeds dispersing less far from their parent. Thus, seeds were likely to land near a conspecific adult regardless of the distance over which they were dispersed. Third, seed crowding increased drastically with adult density, but as a direct consequence of greater seed abundance rather than due to NDD of dispersal. This implies that there is no way for seeds and seedlings to escape from juvenile conspecifics in dense populations, which makes them prone to attack by density-responsive natural enemies.

All tropical trees show aggregation (e.g. Condit *et al.* 2000), and do so at a level that was sufficient for NDD of seed removal in *Virola surinamensis* (Manasse & Howe 1983), suggesting that NDD dispersal could be pervasive if linked with abundance. We expect the consequences of NDD of dispersal for recruitment will depend on the abundances and characteristics of the focal plant species and its dispersers, with NDD of dispersal having important negative consequences in some cases. Unlike our focal species, the vast majority of tropical plant species never reach high local densities, and thus may not reach the point at which dispersal effects on seed distributions become irrelevant. Furthermore, seed handling is important for seed germination and/or escape from seed pathogens and/or predators in many species (e.g. Traveset 1998; Jansen *et al.* 2010). In such species, any decline in seed removal would lead directly to a decline in the proportion of surviving seeds, thus contributing to NDD of recruitment. Finally, we note that our analyses of recruitment success were limited to our plots, ignoring the potential for long-distance dispersal (LDD). Insofar as LDD is also NDD, associated reproductive output will be reduced disproportionately in more dense stands, especially considering that LDD is the only way to escape high local conspecific densities and associated threats in these stands.

Future directions

Clearly, a key question concerns the generality of these results to other plant populations. Despite the voluminous literature on seed dispersal, few studies have reported tests of NDD dispersal, and none have previously quantified its consequences. More studies are needed to establish the frequency of NDD dispersal, to quantify its impacts when present, and to investigate what characteristics of plant populations and their dispersers explain variation in the occurrence of NDD dispersal and in its consequences when present.

AUTHORSHIP

All authors designed the study, M.D.V., G.R. and P.A.J. collected the field data, M.D.V. did the modelling, P.A.J. and M.D.V. analysed the data and drafted the manuscript, all authors contributed substantial revisions.

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