Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species

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Abstract. One of the hypothesized benefits of seed dispersal is to escape density- and distanceresponsive, host-specific, natural enemies near maternal plants where conspecific seed and seedling densities are high. Such high conspecific neighbor densities typically result in lower offspring growth and survival (i.e., negative density-dependent effects), yet many dispersal modes result in clumped seed distributions. New World leaf-nosed bats transport fruits to their feeding roosts and deposit seeds, thereby creating high-density seed/seedling patches beneath feeding roosts in heterospecific trees away from maternal trees, which seemingly nullifies a key benefit of seed dispersal. Such dispersal may still be adaptive if negative density-dependent effects are reduced under feeding roosts or if the benefit of being dispersed away from maternal trees outweighs negative effects of conspecific seed/seedling density below roosts. We mapped the entire post-germination population of a bat-dispersed tree species Calophyllum longifolium (Calophyllaceae) in a 50-ha plot on Barro Colorado Island, Panama in each of three successive years. We tested two hypotheses: (1) distance-dependent effects are stronger than density-dependent effects on seedling performance because seedlings far from conspecific adults are more likely to escape natural enemies even when at high densities and (2) negative density-dependent effects will be reduced far from vs. near conspecific adults. Density and distance were naturally decoupled, as expected. However, in contrast to our expectation, we found positive density effects on seedling survival and density-dependent effects did not differ with distance from conspecific adults. Both density and distance had positive effects on seedling survival when considered together, while only year had a significant effect on seedling growth. Thus, both being dispersed under bat feeding roosts and escaping the vicinity of conspecific adults were beneficial for C. longifolium seedling survival, supporting the directed dispersal and escape hypotheses, respectively. Despite resulting in high densities of conspecific seedlings, favorable habitat under bat feeding roosts and lack of negative density-dependent effects appear to provide evolutionary advantages in C. longifolium.

Key words: bat feeding roost; conspecific adult; density-dependent effects; directed dispersal hypothesis; El Niño; growth; Janzen-Connell hypothesis; pathogen inoculum accumulation; seed dispersal; seedling; spatial pattern; survival.

INTRODUCTION

As sessile organisms, trees frequently depend on various agents to disperse seeds away from maternal trees, typically at the cost of resource investment (Howe and Smallwood 1982). Many studies from both temperate and tropical forests show that offspring often experience high mortality near maternal trees where conspecific seed and seedling densities are high due to host-specific natural enemies (e.g., seed predators, herbivores, pathogens; Comita et al. 2014). Thus, dispersal away from maternal trees leads to increases in offspring performance (survival and growth), known as the Janzen-Connell hypothesis or escape hypothesis (Janzen 1970, Connell 1971, Howe and Smallwood 1982). This negative conspecific density dependence or positive distance dependence in offspring

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performance has been one of the major explanations for the evolutionary advantage of seed dispersal. It is also hypothesized to foster species coexistence; common species encounter higher conspecific densities and therefore should have elevated mortality rates, which gives rare species an advantage and thereby potentially allows more species to coexist in a community (e.g., Harms et al. 2000, Bagchi et al. 2014). Based on these hypotheses, dispersed seeds are expected to have an advantage over undispersed seeds by being deposited in sites with low conspecific seed densities away from maternal trees.

However, many dispersal modes result in a clumped distribution of seeds, which seems maladaptive. Such examples include both biotic and abiotic dispersal modes, such as mounds by ants (Davidson and Morton 1981), cache sites by scatter-hoarding rodents (Vanderwall 1993), song perches of birds (Wenny and Levey 1998), sleeping sites of primates (Russo and Augspurger 2004), latrines of large mammals (Fragoso 1997), as well as wind (Augspurger and Franson 1988) and water (Hart and Cox 1995).

In the tropics, dependence on animal dispersers is known to be particularly high (Howe and Smallwood 1982), which

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suggests that animal dispersal is particularly advantageous evolutionarily in the tropics. Different dispersal agents generate distinct offspring distribution patterns (Howe 1989, Clark et al. 2005), and although dispersal increases offspring distance from maternal trees, density may not always be reduced, and can in fact be concentrated. In the tropics, bats are often the most common mammal (Patterson et al. 2003). To reduce predation risks, some fruit bats such as fruit-eating New World leaf-nosed bats (Phyllostomidae) and African megabats (Pteropodidae) avoid feeding at fruiting trees (Morrison 1980, Seltzer et al. 2013). Instead, they transport one fruit at a time in their mouth to nearby feeding roosts where they defecate and deposit seeds (Janzen et al. 1976, Morrison 1978, Kunz 1982, Howe 1989, Patterson et al. 2003, Marques and Fischer 2009). This feeding habit results in high seed and seedling densities beneath heterospecific feeding roosts away from maternal trees (Janzen et al. 1976, Howe 1989). Consequently, seeds and seedlings of these bat-dispersed species may still suffer high mortality away from maternal trees due to conspecific negative density dependence. Feeding roost behavior would therefore seem to nullify the benefit of seed dispersal, and would appear maladaptive, considering the amount of resources bat-dispersed tree species invest in nutrient-rich fruits.

This "paradox of bat dispersal" (Spiegel and Nathan 2010), as one example of clumped seed dispersal, might be explained if the probability of natural enemy attack was primarily driven by distance to maternal trees, rather than by the local density of conspecific seeds and seedlings. For example, seeds dispersed under bats' feeding roosts away from maternal trees may benefit from escaping pathogens that have accumulated over time in soil under long-lived maternal trees. Experimental studies have shown that soil microbial communities play a key role in causing negative density-dependent effects (e.g., Packer and Clay 2000, Klironomos 2002, Li et al. 2009). Overstory trees can act as reservoirs of pathogens that impair seedling performance (Liang et al. 2016). Repeated high seed input and hence seedling emergence in high densities over multiple fruiting events may also lead to high pathogen accumulation in soil near maternal trees (Augspurger 1990, Packer and Clay 2000), which may thereby create a gradient in pathogen inoculum levels in relation to the distance from maternal trees (Augspurger and Kelly 1984, Augspurger 1990, Packer and Clay 2000, Li et al. 2009). Such an accumulation of host-specific pathogens under bats' feeding roosts is less likely since their location may change frequently (Morrison 1978, 1980, Kunz 1982) and roosts are typically in plants of species different from the species whose fruits they are consuming (Janzen et al. 1976, Morrison 1978, Marques and Fischer 2009). Thus, despite the high conspecific seed and seedling densities encountered, there could still be a benefit of dispersal away from maternal tree to under bat feeding roosts, where pathogen levels may be lower. At the same time, seedlings under bat feeding roosts may benefit from bats removing the pulp (Marques and Fischer 2009) and fertilizing effects of bats' guano (Voigt et al. 2015), which may offset any negative density-dependent effects under bat feeding roosts.

Conspecific density effects on seedling performance may also depend on distance from maternal trees. If a species-specific pathogen accumulates under maternal trees, nearby seedlings would be more likely to become infected by pathogens, because high local conspecific seedling density results in high probability of transmission to neighboring seedlings. If inoculum levels of species-specific pathogens decrease with increasing distance from maternal trees, then seedlings located far from conspecific adults would be less likely to become infected in the first place, and the likelihood of seedling-to-seedling transmission might be reduced despite high conspecific seedling density. In addition, the benefits of being under a bat feeding roost (e.g., higher nutrient input from bat guano; Voigt et al. 2015) may reduce or cancel out negative effects of high density. Some evidence supports such density × distance interactions (Augspurger and Kelly 1984, Yamazaki et al. 2009, Xu et al. 2015). However, most studies have assessed the effects of density and distance independently (Comita et al. 2014), and recent studies have largely focused on conspecific negative density dependence (e.g., Liang et al. 2016, Zhu et al. 2018).

Density and distance are often highly correlated in nature because most seeds end up near maternal trees, which make disentangling the two effects difficult in field experiments (Reinhart and Clay 2009, Xu et al. 2015). Some attempts to assess both density- and distance-dependent effects simultaneously have been experimental (e.g., Augspurger and Kelly 1984, Packer and Clay 2000, Li et al. 2009). Although experimental studies generally allow more direct tests separating hypothesized effects compared to observational studies, experimental conditions may not closely mimic natural conditions (Packer and Clay 2003). Similarly, although arbitrary categorization of density (e.g., "low" vs. "high") and distance (e.g., "near" vs. "far") is common in experimental studies, these categories may not necessarily reflect the biology and scale at which density- and distance-dependent effects operate, or cover a sufficiently wide spectrum or heterogeneity of actual densities or distances. Bat-dispersed tree species, in which density and distance can be naturally decoupled, provides a unique opportunity to disentangle density and distance effects, as well as to explore their potential interaction.

In order to address the paradox of bat dispersal and to examine potential interactive effects of density and distance dependence, we tagged and mapped the entire post-germination population of the bat-dispersed tree species Calophyllum longifolium (Calophyllaceae), within a 50-ha plot in central Panama in each of three successive years. We focused our analyses on seedlings and small saplings (defined as <1 cm dbh, hereafter "seedlings") because density- and distance-dependent effects are often strongest for the smallest size classes (e.g., Zhu et al. 2018), and potential benefits of bat dispersal would most likely be expressed in the earliest life history stages. In addition, by restricting the study to seedlings, we minimized the probability of overestimating the distance to nearest adult tree (i.e., because of mortality of previous nearest adult, which is more likely to have occurred for larger individuals; Sugiyama 2015). Using data on individual seedling survival and growth, in combination with spatial data on all seedlings and trees within the plot, we tested two hypotheses: (1) distance-dependent effects are stronger than density-dependent effects on seedling performance because seedlings far from conspecific adults are

more likely to escape natural enemies even when at high densities and (2) negative density-dependent effects will be reduced far from vs. near conspecific adults (i.e., a significant density \times distance interaction).

METHODS

Study species

We tested our hypotheses using the intermediately shadetolerant (Wright et al. 2003), bat-dispersed, canopy tree species *Calophyllum longifolium*. It is a polygamous, insectpollinated species (Croat 1978, Stacy et al. 1996) that reproduces after reaching 45 cm diameter at breast height (dbh; Visser et al. 2017). *C. longifolium* has three fruiting peaks: in the dry season (March), early wet season (June–July), and late wet season (November–December; Zimmerman et al. 2007). Fruits of *C. longifolium* are green, ~3–4 cm in diameter, and contain one large seed of ~2–3 cm diameter (Croat 1978; A. Sugiyama, *personal observation*).

Fruit-eating bat species, such as the Jamaican fruit bat (Artibeus jamaicensis) and the great fruit-eating bat (Artibeus lituratus), are considered to be the primary dispersers because of the large fruit size (Mello et al. 2005, Marques and Fischer 2009). At feeding roosts, bats scrape the pericarp with their teeth and consume the juice from the fleshy material by chewing the fruit and spitting out most of the remaining pulp (Janzen et al. 1976, Mello et al. 2005, Marques and Fischer 2009) where they deposit the seeds without swallowing them (Appendix S1: Fig. S1). Thus, bats leave the endocarp, seed coat, and endosperm intact after feeding on the fruit (Margues and Fischer 2009). Other mammals, such as white-faced capuchin monkeys (Cebus capucinus; Croat 1978) and Central American agoutis (Dasyprocta punctata; Smythe et al. 1996), also consume its fruits. Tome's spiny rats (Proechimys semispinosus) are known seed predators but a relatively small proportion of seeds is scatterhoarded and larderhoarded (Adler and Kestell 1998) and secondary dispersal is considered to be scarce (P. A. Jansen, personal communication).

Study site and data collection

We conducted this study between 2014 and 2016 in the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama (9°10' N, 79°51' W). The BCI forest mainly consists of semi-deciduous old growth lowland moist forest at an elevation ranging between 120 and 155 m. The forest in the 50-ha plot is considered mostly undisturbed for over 500 yr (Fleming et al. 2009), except for 2 ha of secondary forest along the northeastern edge of the plot. There is a distinct 4-month dry season between January and April (see Croat [1978], Leigh [1999], Losos and Leigh [2004] for detailed descriptions), and annual precipitation during the study was 2,205 mm in 2014, 1,811 mm in 2015, and 2,951 mm in 2106 (S. Paton, *personal communication*). Based on the Oceanic Niño Index, 2015–2016 was a "very strong" El Niño year.

In this study, we combined three data sets. For the location of (reproductive size) adult trees (dbh \ge 45 cm), we used data from a 2015 census of all free-standing woody

plants ≥ 1 cm dbh that were tagged, mapped, and identified in the 50-ha plot (Condit 1998, Hubbell et al. 1999, Condit et al. 2012). In addition to data from the primary tree census, we used seedling census data from 2014 and 2016 in 1×1 m plots that are located in the center of every 5×5 m sub-quadrat of the 50-ha plot. In these 20,000 seedling plots, all free-standing woody plants 20 cm tall to <1 cm dbh have been recorded every one to two years since 2001 (see Comita et al. 2007). In order to have continuous spatial data for seedlings, we also recorded all C. longifolium individuals (including <20 cm tall) outside the seedling plots that had not been recorded in the primary tree census (Appendix S1: Table S1). We tagged, mapped, and recorded size (height and/or dbh, depending on the size) and status (alive/dead) in 2014, 2015, and 2016 (Fig. 1). Recording and mapping all C. longifolium individuals in the 50-ha plot enabled us to capture rare occurrences of seedlings at low densities far away from both maternal trees and feeding roosts; these isolated seedlings might have exceptionally high survival rates (Janzen et al. 1976), which may not be fully captured by sub-sampling.

Statistical analyses

To assess distance effects, we calculated distance to the nearest conspecific adult in 2015 for each seedling alive in 2014 and/or 2015. When the nearest adult was farther than the nearest plot edge, we excluded that seedling from our analyses to avoid overestimating the distance. In addition to continuous distance, we also classified seedlings as "undispersed" (≤ 10 m from the nearest conspecific adult) or "dispersed" (≥ 10 m). The use of 10 m was based on a clear peak of seedling density at < 10 m, with a trough at ~ 10 m (Fig. 2). To assess conspecific density effects, we calculated density at two spatial scales: the number of conspecific seedlings within 2 m and within 5 m for each seedling.

To test the first hypothesis that distance-dependent effects are stronger than density-dependent effects on seedling performance for this bat-dispersed species, we compared models of seedling performance (survival or growth) as a function of either distance to the nearest conspecific adult or density of conspecific seedling neighbors using AIC. We modeled survival across the two-year study period (2014-2016) using generalized linear mixed models (binary function, logit link). For growth, we calculated annual relative growth rate (RGR) as $(\log_{10}[\text{height}_{n+1}] - \log_{10}[\text{height}_n])/$ $(t_{n+1} - t_n) \times 365$, where time t_n was the measurement date at time *n*. When growth was negative due to a broken stem or measurement error, we excluded the data from our analyses. For non-negative growth data, we used Box-Cox transformation as $\log_{10}(\text{height} + \lambda)$, where λ was one-half the smallest positive value. We modeled log₁₀-transformed RGR for both census intervals combined (2014-2015 and 2015-2016) using linear mixed models (Gaussian distribution and identity link).

To test the second hypothesis that negative density-dependent effects decrease with increasing distance from conspecific adults, we ran similar models of seedling survival and growth as a function of both density and distance, with and without a density \times distance interaction term. Prior to the analyses, we confirmed that no multicollinearity existed



FIG. 1. Distribution of all *Calophyllum longifolium* individuals in the Barro Colorado Island (BCI) 50-ha Forest Dynamics Plot, Panama. Adults (\geq 45 cm dbh), juveniles (1–45 cm dbh), and seedlings (<1 cm dbh) are shown in solid red, open gray, and solid blue circles, respectively, reflecting their sizes. Adult and juvenile data are from 2015 and seedling data are from 2014. The contour lines show elevation in 5-m intervals.

between density and distance (variance inflation factor <1.3, condition index <5.2).

Because there may be residual effects of recently deceased conspecific adults, we repeated the same analyses using adult trees from 2010, 2005, and any census year since 1982 (the year of the first full-plot census). However, using adults in 2015 generated better or equivalent ($\Delta AIC < 2$) models than those using adults from previous years based on model comparisons using AIC. Similarly, in all of our analyses, models with density at 5 m scale were better or equivalent than at 2 m scale, and models with categorical distance were consistently better than models with continuous distance (Appendix S1: Table S2). Based on these results, we report models using the 2015 adult data with categorical distance (undispersed, dispersed) and seedling density calculated at 5-m scale in the main text.

For all models, we standardized density and distance prior to analyses. Because initial height may affect seedling performance regardless of density and distance, we also included initial height as a covariate as standardized $\log_{10}(\text{height}_{n-1})$. When only dbh data were recorded (for individuals >1.3 m tall but <1 cm dbh), we used an allometric equa- $\log_{10}(\text{height}) = 0.814 \times \log_{10}(\text{dbh}) + 1.5411$ $(R^2 =$ tion 0.96; height was measured in cm, dbh in mm) based on data from 43 individuals of C. longifolium with measurements for both height and dbh. We used this estimated height only for predicting survival. For all growth analyses, we included only individuals with measured height values. Because C. longifolium juveniles (≥ 1 cm dbh) are known to be associated with slopes in the BCI plot (Condit et al. 1996, Harms et al. 2001), we also included slope habitat as a binary variable in preliminary analyses. However, none of the seedlings from undispersed seeds were on a slope and slope had no effect on performance of seedlings from dispersed seeds (survival P = 0.18, growth P = 0.132), so we did not include it in the final models. We included 20×20 m quadrat as a random effect to account for the nested structure of the data, i.e., seedlings located within the same quadrat are more likely to have similar growth and survival rates compared to seedlings located in different quadrats (Zhu et al. 2018). For all growth models, we also included year as a fixed effect to account for differences between the two census intervals. We also included individual as a random effect in growth models to account for repeated measures on the same individuals. We performed statistical analyses using R 3.4.3 (R Core Team 2017) with lme4 1.1.15 (Bates et al. 2015) and lmerTest 2.0.36 packages (Kuznetsova et al. 2017) and generated predicted intervals using the merTools 0.4.1 R package (Knowles and Frederick 2018).

RESULTS

After excluding individuals near plot edges, we had data on 4,012 naturally occurring seedlings in the BCI 50-ha plot in 2014 (Appendix S1: Table S1). Although 3.6% of seedlings occurred under only five conspecific adult trees, we found the majority of seedlings more widely dispersed (Fig. 1). Seedlings occurred up to about 180 m from the nearest conspecific adult (Fig. 2). As expected, density and distance were decoupled in *C. longifolium*; the distribution of seedling density was not unimodal and exhibited multiple peaks at different distances from conspecific adults (Appendix S1: Fig. S2). Multimodal distributions persisted during the three years of this study, but the persistence of these peaks varied by distance and with spatial scale.

When comparing models with conspecific seedling density to models with distance to nearest conspecific adult, density was a better predictor of seedling survival than distance in *C. longifolium*, in contrast to our first hypothesis (Table 1). However, contrary to expectation, conspecific seedling density effects on seedling survival were positive. Neither density nor distance alone were significant predictors of seedling growth, and only year had a significant effect in the growth models.



FIG. 2. Relationship between distance to the nearest conspecific adult and conspecific seedling neighbor density within 5 m for *C. longifolium* seedlings (<1 cm dbh) in (a) 2014, (b) 2015, and (c) 2016. We calculated distance to nearest adult using adult data from 2015. Dashed vertical lines at 10 m from the nearest conspecific adult shows the threshold for which we classified seedlings into "undispersed" and "dispersed." Density at the 2-m scale is shown in Appendix S1: Fig. S2.

In contrast to our second hypothesis that negative density-dependent effects are reduced away from conspecific adults, there was no significant density \times distance interaction (survival P = 0.563, growth P = 0.140; Table 1, Fig. 3). Instead, the best model for survival included both density and distance, but not their interaction, with the probability of survival increasing with both increasing density of conspecific seedlings and increasing distance to nearest conspecific adult. For growth, only year had a negative effect in models including both distance and density.

DISCUSSION

The existence of many bat-dispersed tropical tree species suggests evolutionary advantages to bat dispersal, but high densities of seeds dispersed under bat feeding roosts could potentially offset the benefits of seed dispersal. Using demographic data from a fully mapped tree population, we showed that conspecific seedling density did not reduce seedling performance of the bat-dispersed species *C. longifolium*. Rather, both dispersal away from conspecific adults and conspecific seedling density effects improved initial survival in this species. Thus, our results resolve the "paradox of bat dispersal": seeds dispersed by bats appear to benefit from being moved away from conspecific adult trees and, at the same time, thrive at high conspecific seedling densities found beneath bat feeding roosts, at least during the seedling stage.

In a recent meta-analysis studying density dependence, increasing conspecific density was found to have an overall negative impact on seedling survival (although individual species effects included both positive and negative density effects; Comita et al. 2014). However, in our study, conspecific seedling density had a positive effect on seedling survival in C. longifolium, i.e., seedling survival was more likely in areas of high conspecific seedling density. Such high areas of conspecific seedling density in this species should occur under conspecific adults or bat feeding roosts. Dispersal away from conspecific adults also had a positive effect on seedling survival in models that included both dispersal and density. Thus, high seedling patches under bat feeding roosts and not under conspecific adults most likely led us to detect positive density effects, although we did not study the underlying mechanism. Supporting this idea, when analyzing seedlings from undispersed vs. dispersed seeds separately, we found significant positive density effects on survival only for seedlings from dispersed seeds (0.26, P = 0.0006) and not undispersed seeds (0.14, P = 0.40), suggesting that dispersal specifically to bat feeding roosts, and not simply high seedling density, is beneficial for C. longifolium. However, this pattern may not hold for all bat-dispersed species or stages. For example, in the bat-dispersed species Andira inermis (Fabaceae) in Costa Rica, mortality due to seed predation was higher under maternal trees than feeding roosts, but lowest for seeds dropped between maternal trees and feeding roosts (Janzen et al. 1976). Although seeds of multiple bat-dispersed species with overlapping phenology are deposited under bat feeding roosts (Seltzer et al. 2013), heterospecific seedling interactions were likely negligible (Comita et al. 2010).

For survival, the best model included significant positive effects of both conspecific seedling density and dispersal away from conspecific adults. Enhanced survival by being dispersed away from conspecific adults supports the escape hypothesis (Howe and Smallwood 1982). Indeed, survival of C. longifolium seedlings was overall low near conspecific adults (Appendix S1: Fig. S3). Low seedling survival beneath conspecific adults could result from host-specific pathogen accumulation and/or asymmetric resource competition between adults and seedlings of the same species. If mortality is high near conspecific adults regardless of seedling density (i.e., lack of negative density-dependent effects) due to high pathogen inoculum level (Augspurger and Kelly 1984), dispersal away from conspecific adults would increase the probability that seedlings escape these negative impacts. At the same time, enhanced survival when dispersed under bat feeding roosts supports the directed dispersal hypothesis, which proposes that an advantage of seed dispersal is enhanced performance of seeds dispersed to non-random, favorable habitats by animals (Howe and Smallwood 1982).

TABLE 1. Summary of best density-only model (hypothesis 1), distance-only model (hypothesis 1), and full model (hypothesis 2) predicting 2-yr survival (2014–2016) and height relative growth rate (RGR; 2014–2015 and 2015–2016) for *C. longifolium* seedlings based on the Akaike information criterion (AIC).

Fixed effects	Estimate	SE	Ζ	Р	P
2-yr seedling survival (2014–2016)					
Best density-only model (AIC = $3,143$)					
Intercept	1.24	0.08	15.46		< 0.0001
Density	0.17	0.07	2.52		0.01
Initial height	0.81	0.06	13.78		< 0.0001
Best distance-only model (AIC = $3,146$)					
Intercept	0.74	0.24	3.09		0.00
Distance	0.45	0.24	1.91		0.06
Initial height	0.78	0.06	13.36		< 0.0001
Best density and distance model (AIC = $3,141$)					
Intercept	0.77	0.24	3.25		0.00
Density	0.17	0.07	2.65		0.01
Distance	0.48	0.23	2.08		0.04
Initial height	0.80	0.06	13.68		< 0.0001
Seedling growth (2014–2015 and 2015–2016)			df	t	
Best density-only model (AIC = $3,909$)					
Intercept	-1.44	0.03	148.9	-47.93	< 0.0001
Density	-0.01	0.02	867.8	-0.61	0.54
Initial height	-0.02	0.02	1,352.4	-1.26	0.21
Year (2015–2016)	-0.11	0.03	1,069.3	-4.32	< 0.0001
Best distance-only model (AIC = $3,906$)					
Intercept	-1.50	0.09	828.2	-17.52	< 0.0001
Distance	0.07	0.08	1,031.8	0.88	0.38
Initial height	-0.02	0.02	1,329.9	-1.23	0.22
Year (2015–2016)	-0.11	0.03	1,070.4	-4.32	< 0.0001
Best density and distance model (AIC = $3,914$)					
Intercept	-1.51	0.09	761.5	-17.46	< 0.0001
Density	-0.01	0.02	855.4	-0.64	0.52
Distance	0.08	0.08	1,026.2	0.90	0.37
Initial height	-0.02	0.02	1,352.5	-1.27	0.20
Year (2015–2016)	-0.11	0.03	1,069.4	-4.32	< 0.0001

Notes: Density is at the 5-m scale and distance is categorical (undispersed ≤ 10 m and dispersed >10 m from the nearest conspecific adult). Density \times distance interactions were not significant (survival P = 0.56, growth P = 0.14). Variable estimates in boldface type are significant at $\alpha = 0.05$. A list of all models is in Appendix S1: Table S2.

While several studies have examined directed dispersal in the context of dispersal to light gaps (e.g., Wenny and Levey 1998, Haurez et al. 2015), enhanced seedling survival under bat feeding roosts is unlikely to result from elevated light levels because bats avoid gaps, potentially due to higher visibility to their predators, and feed in subcanopies, 5-15 m above the ground (D. W. Morrison, personal communication). A perhaps more likely explanation for favorable roost habitats is the fertilizing effects of bats' guano, which would increase nutrient availability beneath roosts (Voigt et al. 2015). Similar fertilizing effects may be expected for seeds deposited in dung, which may serve as another example of directed dispersal, although those seeds may experience high removal rates and whether benefits outweigh the cost of seed caching from directed dispersal is likely species dependent (reviewed in Wenny [2001]).

The lack of negative density-dependent effects in seedlings of *C. longifolium* is contrary to many studies reporting pervasive negative conspecific density dependence in tropical tree seedlings (e.g., Harms et al. 2000, Bagchi et al. 2014). However, if bat-dispersed tree species are adapted to being deposited in high density, they may not experience negative

conspecific density-dependent effects (Howe 1989). Lack of negative density effects in seedling survival under bat feeding roost or under conspecific adults may also be explained by the life history of C. longifolium, which is moderately shade tolerant (Wright et al. 2003) and has relatively large seeds. Slower-growing, shade-tolerant, tropical tree species tend to be less susceptible to conspecific density-dependent effects (Kobe and Vriesendorp 2011, Zhu et al. 2018). Similarly, seedlings of large-seeded species better tolerate negative density-dependent effects than small-seeded, fastgrowing, tree species (Lebrija-Trejos et al. 2016). In fact, little conspecific, negative density-dependent effects were found for C. longifolium in a previous study of first-year survival of seedlings in the BCI community (E. Lebrija-Trejos, personal communication). It is possible that some of our shade-suppressed seedlings <1 cm dbh were decades old (Clark and Clark 2001). If so, some of the peaks in the density of seedlings as a function of distance to nearest conspecific adult could have resulted from maternal trees that died before 1982, whose data we do not have. However, these multimodal patterns of distance to nearest adult persisted even when we restricted the seedling size to ≤ 50 cm tall



FIG. 3. Predicted effect of conspecific seedling density on 2-yr survival for *C. longifolium* seedlings from undispersed and dispersed seeds based on the best fit survival model (see Table 1). Black lines indicate median predicted values and gray lines indicate 90% prediction intervals based on fixed variation from 5,000 simulation samples.

(Appendix S1: Fig. S4), suggesting that these peaks largely reflect recent recruits and result from bats' behavior.

Another potential explanation for the lack of negative conspecific density-dependent effects in our study is that it coincided with a severe El Niño-related drought during the 2015-2016 dry season. C. longifolium is known to be highly drought sensitive compared to other tree species on BCI (Engelbrecht et al. 2007). Indeed, we observed many saplings that were standing dry and dead, and even live adults had many dry leaves and branches between 2015 and 2016 (A. Sugiyama, personal observation). C. longifolium seedling growth was also significantly lower in 2015-2016 compared to 2014–2015 (Table 1). Thus, drought impacts on seedling performance during our study may have over-ridden the negative effects on conspecific density. Such drought years may also reduce pathogen activity (Augspurger 1984, Augspurger and Kelly 1984, Swinfield et al. 2012), which may result in reduced negative effects of conspecific density dependence via soil-borne pathogens (Augspurger and Kelly 1984, Swinfield et al. 2012).

Bats' selection of feeding roosts should have a major impact on structuring the *C. longifolium* population. Potential dispersers of *C. longifolium*, *A. jamaicensis*, and *A. lituratus* are non-permanent, foliage-roosting bats, and show more fidelity to home area rather than specific roosts (Kunz 1982), where they use the same feeding area of 0.25–0.5 ha on BCI (Morrison 1978). Such unpredictable and frequent changes in feeding roost locations should limit the ability of host-specific enemies to "track" high density patches of seedlings, which may also make seedlings less susceptible to negative densitydependent effects. Even if negative density-dependent effects occurred under bat feeding roosts, if a small proportion of seeds accidentally dropped by bats during transportation between maternal trees and roosts show exceptionally high survival, it may outweigh other costs and make bat dispersal adaptive. These bat behaviors may further reinforce an evolutionary advantage favoring species that have bats as seed dispersers.

Although our results based on the seedling stage revealed some benefits of bat dispersal, different mechanisms may act at different stages (e.g., Schupp 1995). At the seed stage, pulp removal by bats promoted germination in a congener C. brasiliense, whereas no seeds germinated when >75% of pulp remained (Marques and Fischer 2009). Pulp removal also led to faster germination, which reduces seed predation and pathogen infection (Margues and Fischer 2009). Our study suggests continued benefits of bat dispersal at the seedling stage, with higher initial survival at high conspecific densities beneath bat feeding roosts. If positive density effects under bat feeding roosts persist to the adult stage, we should see clumps of adults. However, adults were mostly scattered widely across the plot, whereas juveniles (1-45 cm dbh) were more aggregated with little overlap with adults (Fig. 1). Similarly, seedlings were often more aggregated and closer to adults than juveniles. However, in a large tree species such as C. longifolium, multiple seedlings cannot all mature into reproductive adults within a single meter square due to space limitation. In addition, continuing positive distance-dependent effects will likely reduce survival in clumps as seedlings grow larger, and may shift recruits away from adults over time (Sugiyama 2015), which may lead to spatial separation of different size classes. In fact, growth of C. longifolium saplings (2 cm dbh) is known to be reduced by conspecific neighbors (Uriarte et al. 2004). Sensitivity to environmental stress may also change with life stage. Thus, the benefits of bat dispersal at early life stages may be reduced by processes occurring at later stages (such as intraspecific competition). Although little is known about multi-stage effects of negative density dependence for batdispersed species, spatial aggregation due to initial dispersal failure led to negative density dependence across all life stages and major demographic consequences in other animal-dispersed tree species (Caughlin et al. 2015). Whether our results apply at later stages and lead to long-term benefits of bat dispersal requires further work.

In the 50-ha plot on BCI, 85% of all woody species recorded in the main censuses to date with known dispersal modes are animal-dispersed, 18% of which are bat-dispersed (Wright et al. 2016). At least for the seedling stage, the apparent paradox of clumped dispersal in one such species can be explained by positive dispersal effects, especially to under bat feeding roosts where seedling survival was enhanced, combined with a lack of negative density-dependent effects. The multimodal patterns of dispersal distances we observed in this bat-dispersed species may also be observed in other animal-dispersed species, such as nests of ants (Davidson and Morton 1981), cache sites of chipmunks (Vanderwall 1993), song perches of Bellbirds (Wenny and Levey 1998), sleeping sites of monkeys (Russo and Augspurger 2004), and latrines of tapirs (Fragoso 1997). Thus, our findings may apply to a broader suite of clumped-dispersed species than previously assumed. Better understanding of the long-term consequences of disperser behavior and potentially different mechanisms acting on various life stages may further improve our understanding of the high

dependence on animal dispersers and how plant communities are structured in tropical forests.

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