



Botanical Journal of the Linnean Society, 2016. With 4 figures

# Relative influence of relatedness, conspecific density and microhabitat on seedling survival and growth of an animal-dispersed Neotropical palm, *Oenocarpus bataua*

JORDAN KARUBIAN<sup>1,2\*</sup>, LUKE BROWNE<sup>1,2</sup>, DOMINGO CABRERA<sup>2</sup>, MALINDA CHAMBERS<sup>1</sup> and JORGE OLIVO<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Tulane University, 400 Lindy Boggs Center, New Orleans, LA 70118-5698, USA

<sup>2</sup>Foundation for the Conservation of the Tropical Andes, Quito, Ecuador

Received 9 December 2015; revised 24 February 2016; accepted for publication 20 April 2016

We report on a 6-year, field-based experiment in north-western Ecuador, evaluating the relative importance of relatedness, conspecific density and microhabitat on the growth and survival of seedlings of an ecologically and economically important palm, *Oenocarpus bataua*. We planted *O. bataua* seedlings in high-density seed deposition sites (leks) of the long-wattled umbrellabird (*Cephalopterus penduliger*) and randomly selected control sites. We analysed seedling performance in relation to conspecific relatedness, conspecific density and microhabitat. Among the parameters we measured, light availability was the most important determinant for survival and growth. Higher relatedness of neighbouring experimental seedlings and higher conspecific seedling densities were both associated with reduced growth, but did not influence survival, even in umbrellabird leks. These findings are consistent with a survival advantage of umbrellabird dispersal into lek sites (i.e. directed dispersal) that counterbalances negative density-dependent processes expected to occur at these high-density deposition sites. This study highlights the importance of a multi-tiered approach to understanding palm demography and underlines the importance of seed disperser behaviour in determining seedling fate. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016

**ADDITIONAL KEYWORDS:** Arecaceae – Chocó rainforest – directed seed dispersal – Ecuador – Janzen–Connell hypothesis – lek – negative density dependence.

## INTRODUCTION

Identifying the factors that regulate seedling demography improves our understanding of the mechanistic processes that govern patterns of species and genetic diversity in plants (Schupp & Fuentes, 1995; Rodriguez-Perez & Traveset, 2007). Animal-mediated seed dispersal (zoochory) creates the template upon which post-dispersal demographic processes act for many plant species (Nathan & Muller-Landau, 2000; Wang & Smith, 2002) and is often non-random in terms of the microhabitat and conspecific neighbourhood where seeds are deposited (Schupp, Jordano & Maria, 2010). The microhabitat (e.g. light, soil, hydrology) and density of nearby conspecifics at seed deposition sites are known important drivers of seedling demography (Janzen, 1970; Augspurger, 1984;

Queenborough *et al.*, 2007; Comita *et al.*, 2010; Mangan *et al.*, 2010; Alvarez-Loayza & Terborgh, 2011; Andersen, Turner & Dalling, 2014). In contrast, the ways in which variability in the degree of genetic relatedness within groups of seedlings impacts survival and growth remain unclear (Garcia & Grivet, 2011) and few studies have attempted to simultaneously gauge the relative influence of microhabitat, conspecific density and relatedness for seedling survival. For this reason, more information on demographic dynamics at animal seed deposition sites in relation to these factors would be useful for improving our mechanistic understanding of observed distributions of plant species and community dynamics at the local scale.

Most frugivorous animals use certain sites repeatedly (e.g. latrines, resting sites or display areas) and generate high densities of dispersed seeds at these sites (i.e. ‘contagious’ or ‘destination-based’ seed

\*Corresponding author: E-mail: jk@tulane.edu

dispersal; Howe, 1989; Russo & Augspurger, 2004; Karubian & Durães, 2009). Howe & Smallwood (1982) predicted that seed dispersal might be adaptive for plants if these deposition sites are favourable for establishment (directed dispersal hypothesis). In a classic example, directed dispersal into high-light environments such as forest gaps by bellbirds promoted seed survival (Wenny & Levey, 1998). However, if directed dispersal also leads to higher densities of seeds and seedlings, survival may often be lower at these high-density sites due to higher levels of negative density-dependent (NDD) mortality (Harms *et al.*, 2000; Terborgh, 2012; Bagchi *et al.*, 2014). Although there is convincing evidence that NDD mortality operates close to source trees, the relative importance of this process at sites away from source trees is unclear (Comita *et al.*, 2014). Resolving the relative strength of NDD mortality at repeatedly used dispersal sites vs. the potential benefits of directed dispersal is therefore essential for understanding how zochory influences plant demography (Spiegel & Nathan, 2010).

The genetic composition of frugivore-dispersed seeds at these dispersal sites appears to vary widely across systems, with potentially important consequences for survival and growth trajectories. Some dispersal agents or behaviours create pools of dispersed seeds and seedlings that originate from only one or a few source plants, leading to genetic bottlenecks at these deposition sites (e.g. Grivet, Smouse & Sork, 2005; Karubian *et al.*, 2015), whereas others generate pools of dispersed seeds and seedlings that originate from multiple sources and are quite diverse genetically (e.g. Jordano *et al.*, 2007; Garcia & Grivet, 2011; Scofield *et al.*, 2012). There are three main ecological mechanisms by which genetic relatedness is thought to influence plant performance: susceptibility to attack, kin selection and niche partitioning (File, Murphy & Dudley, 2012). The susceptibility to attack hypothesis suggests that genetic homogeneity among neighbours may increase the probability of attack by herbivores or pathogens. The kin selection hypothesis posits that related plants cooperate better than do groups of strangers and, as a result, that groups of related individuals should enjoy a performance advantage. In contrast, the niche-partitioning hypothesis predicts that related plants overlap to a greater degree in resource use, increasing competition and reducing performance. Many studies to date from natural systems support the niche partitioning perspective (e.g. Milla *et al.*, 2009; Cheplick & Kane, 2010). There is experimental evidence that relatedness among spatially proximate seedlings may also mediate survival (Liu *et al.*, 2015), but little is known about how relatedness, microhabitat and NDD processes may interact to influence seedling

demography in the context of contagious seed dispersal.

In north-western Ecuador, male long-wattled umbrellabirds (*Cephalopterus penduliger*; hereafter umbrellabirds) disperse seeds of preferred fruit species in high densities beneath traditionally used display perches in lek sites, an example of contagious seed dispersal (Karubian *et al.*, 2012). Somewhat surprisingly given strong support for NDD processes from other systems (above), high conspecific densities of seeds and seedlings in umbrellabird leks do not appear to be associated with any detectable survival cost at these sites relative to lower-density 'control' sites outside leks (Karubian *et al.*, 2012). Male umbrellabirds forage at multiple trees surrounding the lek and then deposit these seeds at the lek, leading to high maternal seed source diversity in seed pools at leks relative to randomly dispersed seed pools at control sites (Karubian *et al.*, 2010). Karubian *et al.* (2010) proposed that this high genetic variability may promote seed and seedling survival in umbrellabird leks despite high densities, but this proposition remains untested. Alternatively, it may be the case that microhabitat varies between leks vs. control areas in ways that compensate for any NDD processes that may occur in leks, but again this possibility has not been explored. Resolving the linkages between umbrellabird dispersal, microhabitat and conspecific neighbourhood environment and seedling performance therefore provides a useful context in which to improve our understanding of the mechanistic processes underlying plant demography and resulting patterns of diversity.

In the present study, we report on the results of a field-based experiment designed to assess the relative importance of microhabitat, conspecific density and relatedness on survival and growth of seedlings of the Neotropical palm *Oenocarpus bataua* Mart. We use the term 'seedling' throughout the article to refer to small juvenile plants with or without the cotyledon. Our study design compares growth and survival of seedlings experimentally planted in umbrellabird leks or in control areas outside umbrellabird leks. Based on previous work on palms and other groups, we predicted increased survival and growth in relation to increased light and reduced conspecific density. We also predicted that increased relatedness to neighbouring conspecific seedlings might be associated with reduced survival probability and growth, consistent with niche partitioning. Based on our previous work in this system (above), we predicted increased or equivalent survival and performance in leks relative to control sites, reasoning that more favourable values of light and relatedness in lek sites may outweigh the costs associated with higher densities. Our findings indicate that

light availability drives observed differences in *O. bataua* seedling survival and growth and that relatedness among neighbouring individuals and conspecific density both influence growth, but not survival. Thus, despite higher levels of conspecific density in lek sites, rates of survival are comparable to that of controls, suggesting the existence of some compensatory advantage that balances expected NDD processes in the lek and promotes seedling survival.

## METHODS

### STUDY AREA AND ORGANISMS

The study took place in the 3500-ha Bilsa Biological Station (BBS; 79°45'W, 0°22'N, 330–730 m a.s.l.), located in the Mache-Chindul Mountains in the province of Esmeraldas in north-western Ecuador. BBS lies in the southern portion of the Chocó biogeographical zone, a region characterized by exceptionally high diversity in flora (Gentry, 1992), birds (Carrasco *et al.*, 2013), amphibians (Ortega-Andrade *et al.*, 2010; Jongasma *et al.*, 2014) and other groups.

Our study organism, the canopy palm *O. bataua*, is widely distributed throughout Neotropical rain forest (ter Steege *et al.*, 2013). It is a long-lived, slow-growing monoecious species that produces inflorescences of thousands of small flowers, and is effectively outcrossed (Ottewell *et al.*, 2012). Fertilized flowers develop large-seeded, lipid-rich fruits (up to 2000 fruits per infructescence) that are consumed and dispersed by a range of large-bodied vertebrates, including birds, primates and humans. Seeds require 1–2 months to germinate and germination rates in nursery conditions are high (> 95%) regardless of whether the aril is removed (J. Karubian, unpubl. data). *Oenocarpus bataua* is common at BBS, where density is approximately two adults per hectare (Ottewell *et al.*, 2012).

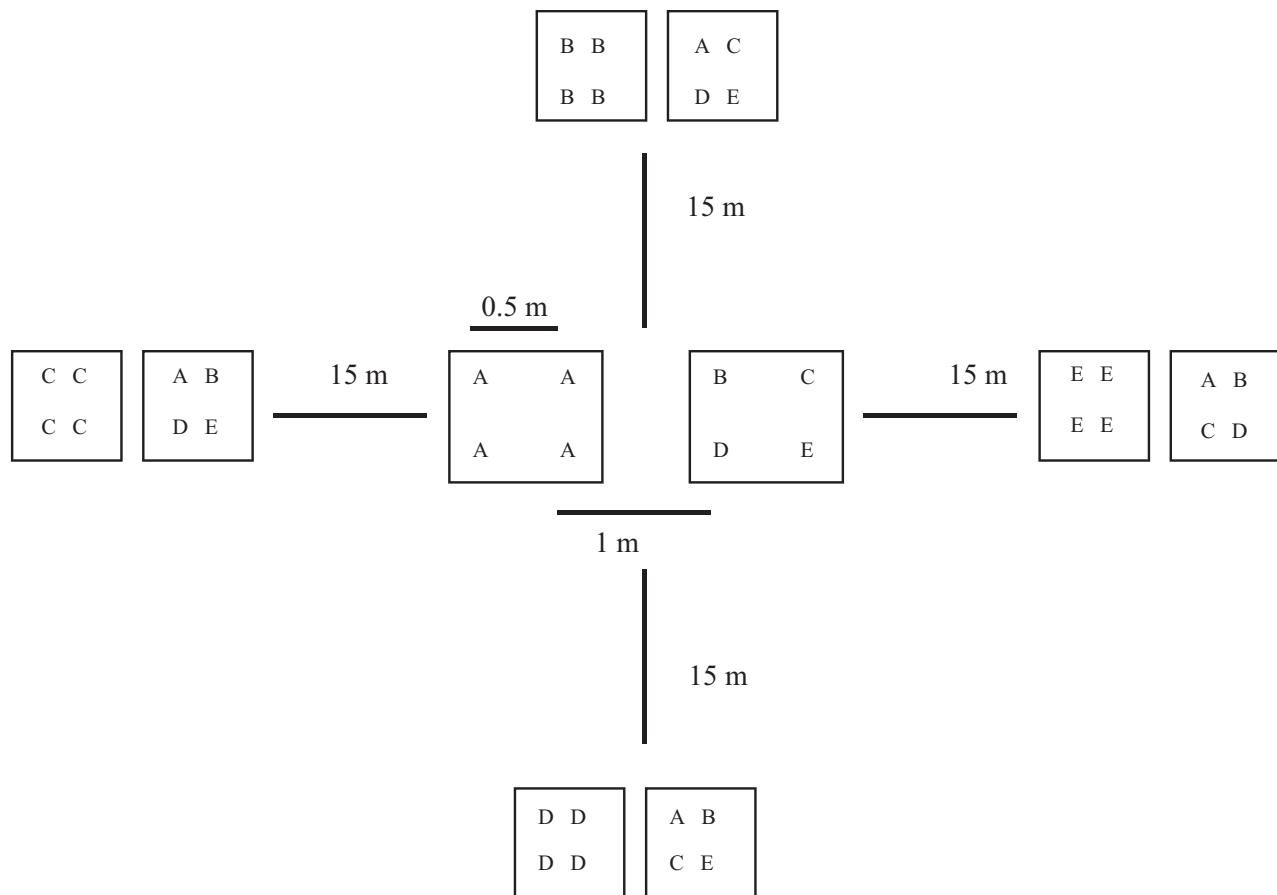
Umbrellabirds are large-bodied (*c.* 550 g) frugivorous birds endemic to the Chocó and are considered by the IUCN as vulnerable to extinction (IUCN, 2015). At BBS, umbrellabirds remove a significant proportion of ripe *O. bataua* fruits by ingesting fruits whole and regurgitating the seeds intact 1–4 h after ingestion (J. Karubian, unpubl. data; Karubian *et al.*, 2012). When not foraging, male umbrellabirds aggregate in lek breeding sites that are active year-round; we have monitored seven leks in BBS since 2005, all of which are included in the current study. Most adult males hold fixed territories at a single lek, although some ‘floater’ males move between multiple leks (Karubian *et al.*, 2012; Karubian & Durães, 2014). Males disperse > 50% of the seeds they ingest into leks (Karubian *et al.*, 2012), yielding

significantly higher densities of seeds and seedlings of *O. bataua* and other preferred fruit species at lek sites than at randomly selected control sites outside the lek. Umbrellabirds also generate diverse seed pools representing multiple maternal source trees at leks (Karubian *et al.*, 2010; Scofield *et al.*, 2012). Correlational analyses detected no evidence of elevated mortality associated with high seed densities within the lek and the probability of transition from seed to seedling did not differ between leks and control sites (Karubian *et al.*, 2012).

### EXPERIMENTAL DESIGN AND FIELD METHODS

We obtained the seedlings used in the current study as part of an earlier investigation of pollen flow in *O. bataua* (Ottewell *et al.*, 2012). Mature *O. bataua* fruits were collected directly from infructescences on adult trees in BBS from May to June 2008 and allowed to germinate individually in 0.5-L plastic bags; soil was collected from multiple locations in BBS and thoroughly mixed before filling individual bags. Germination and subsequent growth took place in a common garden nursery located at forest edge, in dappled sunlight. In September 2008, when seedlings were 3–4 months old, they were transplanted in the field. At the time of planting, all seedlings measured 30–60 cm in total height, had two or three leaves, and were within 1 month of age of each other; our experiment was designed to control for any differences in these measures that may have existed at the time of planting (below, Fig. 1). Seedlings were planted in the forest by removing *c.* 1.0 L of soil with a hand shovel, carefully removing the seedling from the plastic bag in which it was germinated so as to keep most of the soil intact in the bag and placing the seedling and soil in the hole with some of the local soil. At the time of planting, each seedling was marked with an aluminium tag inscribed with a unique field number. There was no evidence of a ‘transplant effect’ (i.e. increased mortality in year 1 associated with transplant) and results were qualitatively similar when excluding the first year of data from our analyses.

Our study design was established to partition the relative importance of location (i.e. leks vs. ‘control’ sites outside the lek), relatedness (i.e. related vs. unrelated to surrounding experimental seedlings), conspecific density (a continuous measure of naturally occurring individuals surrounding experimental seedlings) and microhabitat on survival and growth of *O. bataua* seedlings. The experimental design employed a total of 560 seedlings sourced from 30 adult *O. bataua* trees ( $N = 16$  seedlings from each of 25 adult trees;  $N = 32$  seedlings from each of the remaining five adult trees). All adult source trees



**Figure 1.** Diagram of the planting design (not to scale), replicated across each of 14 sites. The letter variables represent seedlings that share mother trees. In each of five plots, there is a set of four related (same letter) and four unrelated (different letters) seedlings. Each of the four distal plots is located 15 m north, south, east and west of the central plot. We used this study design to monitor growth and survival of 560 experimentally planted seedlings of the canopy palm species *Oenocarpus bataua* in north-western Ecuador from 2008 to 2014.

were located in a 1-km<sup>2</sup> area in BBS. We placed seedlings in each of seven active umbrellabird leks, each of which was c. 1 ha, and seven ‘control’ sites. Control sites were obtained by randomly selecting  $x$ ,  $y$  coordinates within the polygon bounded by the seven focal leks; mean pairwise distance between each control plot and the nearest lek was 620 m. All experimental sites were located in contiguous forest that contained a complex matrix of primary, selectively logged and secondary habitat types. In each of these 14 sites, we set up five experimental seedling plots in a star design, with a central plot and four distal plots to the north, south, east and west (Fig. 1). The distance between the central plot and each of the four distal plots was 15 m. Each plot contained eight seedlings in total: four related seedlings and four unrelated seedlings (below). In each plot, related and unrelated seedlings were planted in discrete 0.5-m<sup>2</sup> areas; each individual seedling was

separated from its nearest neighbour by 0.5 m and the related vs. unrelated subplots were separated from each other by 1.0 m (these subplots were not treated as independent units). We used eight seedlings from each of five source trees in each of our 14 locations, for a total of 40 seedlings per location  $\times$  14 locations = 560 seedlings. Seedling survival and growth were monitored via censuses at 9- to 12-month intervals following planting from September 2008 to July 2014, for a total of six census points. We recorded whether each seedling was alive or dead during each census; if alive, we recorded total height from base to tip of the longest leaf and the total leaf number.

#### PREDICTOR VARIABLES

For the variable ‘location’, we assigned each of our 14 sites as either an umbrellabird lek or control. For

the variable ‘related’, we distinguished between related seedlings we knew to be either full- or half-sibs (i.e. because they were collected as fruit from the same maternal tree; above) vs. unrelated seedlings that were initially collected from different adult trees. This classification scheme does not consider the identity of the pollen source for each seed, so it is possible that two seedlings that we treated as unrelated because they were collected from different source trees actually shared the same sire. However, because this study population is known to be highly outcrossed and to exhibit relatively high pollen source diversity among progeny arrays (Ottewell *et al.*, 2012), this binary metric of relatedness probably reflects a meaningful difference in degree of relatedness among seedlings.

Conspecific density was recorded at each of the five experimental plots per site, yielding 70 data points in total. To measure conspecific density, we recorded the number of *O. bataua* seedlings and juveniles within the entire area of a 5-m-radius circle around the centre of each paired plot in 2008. We also counted the number of adults occurring within a 5-m-radius circle around each plot, a distance that we considered to be appropriate because NDD effects are most pronounced in close proximity to conspecific adults (Janzen, 1970).

Environmental data were also recorded at each of our 70 experimental plots. We used data collected in 2008 (i.e. when the seedlings were planted) for statistical analysis presented below because initial conditions seemed most likely to influence survival (see Results); we also replicated all analyses using 2014 environmental data and recovered qualitatively similar results to those presented below. Canopy cover was measured using a concave spherical densiometer (Forestry Suppliers no. 43888) from the centre of each plot. The number of cells (96 total) containing a majority of canopy were scored and multiplied by 1.04 to arrive at a score potentially ranging from 0 (i.e. completely open) to 100 (i.e. completely closed canopy). Independent measures were taken in each of the four cardinal directions and then averaged for a single score for each plot. The number of large trees, which we used as another measure of canopy cover as well as forest structure, was calculated by counting the number of trees with a diameter at breast height (dbh) > 50 cm within a 10-m radius of each plot. Canopy height was estimated visually after training with a digital range finder. Slope (a variable we did not include in most analyses; see below) was measured in degrees using a clinometer pointed across the steepest transect of the paired plot, and elevation was recorded at each paired plot using a handheld GPS units with error of  $\pm 10$  m a.s.l. We were not able to measure soil chemistry or

hydrology, two environmental factors that may be important for palm recruitment (Eiserhardt *et al.*, 2011).

#### STATISTICAL ANALYSES

We modelled the survival and growth of *O. bataua* seedlings using generalized linear mixed models (Bolker *et al.*, 2009). Because we were interested in the relative effects of location (i.e. lek vs. control), relatedness, conspecific density and microhabitat, we included the following variables as fixed effects in our initial models: location (binary: planted in lek = 1, planted in control sites = 0), related (binary: planted with related seedlings = 1, or not = 0), canopy cover, whether there was at least one tree > 50 cm dbh within a 10-m radius (binary), canopy height, slope, elevation, whether there was at least one adult *O. bataua* in a 5-m radius (binary), and the number of *O. bataua* seedlings and juveniles in a 5-m radius. We included plot nested within site ( $N = 70$ ) and site ( $N = 14$ ) as random effects to account for the dependence between individuals planted in the same plot and to account for unmeasured environmental variables at each plot and site. We also used maternal tree identity ( $N = 30$ ) as a random effect to account for potential unmeasured genetic characteristics among half- or full-siblings that share a common mother. We modelled survival (whether a seedling survived from 2008 to 2014) with a binomial error structure, height in 2014 with a Gaussian error structure (a standard linear mixed model) and total number of leaves in 2014 with a Poisson error structure (Bolker *et al.*, 2009). We then tested for differences in microhabitat and conspecific neighbourhood characteristics between lek and control sites using plots as sampling units ( $N = 70$ ) and site as a random effect ( $N = 14$ ). For each microhabitat and conspecific neighbourhood characteristic, we ran a separate model with lek vs. non-lek as a binary predictor and the characteristic as the response variable, for a total of six models. The number of seedlings and juveniles within a 5-m radius was modelled using Poisson error structure, and trees > 50 cm dbh and number of adults within 5 m were modelled with a binomial error structure. All other habitat and conspecific neighbourhood characteristics were modelled using a standard linear mixed model with a Gaussian error structure.

Models were fitted in the R package lme4 (Bates *et al.*, 2015). We assessed model residuals for deviations from model assumptions (Bolker *et al.*, 2009). A moderately strong correlation between slope and the number of seedlings and juveniles within 5 m ( $r = -0.45$ ,  $t = -4.20$ ,  $df = 68$ ,  $P < 0.001$ ) yielded a variance inflation factor (VIF) greater than the

VIF = 2 threshold suggested by Zuur, Ieno & Elphick (2010), beyond which point collinearity between predictor variables can lead to low power in detecting weak ecological effects. The most effective way to address this issue is to remove one of the collinear variables from the models (Zuur *et al.*, 2010). As one of the core goals of this study was to assess the effects of *O. bataua* densities on seedling growth and survival, we elected to remove slope from analyses and retain conspecific seed and seedling density as a predictor variable. No other predictor variables had a VIF > 2 for any model.

Continuous covariates were mean centred and standardized by dividing by two standard deviations (SD) prior to analyses to aid in model convergence, to allow direct comparison of regression coefficients of binary and continuous covariates and to standardize effect sizes, which can be used as a point of comparison in future studies (Gelman, 2008; Schielzeth, 2010). After scaling, regression coefficients can be interpreted as the difference in log odds of survival (survival model), difference in height (height model) or, when exponentiated, the difference in number of leaves (leaf growth model) for a 2-SD increase in a predictor variable. Because covariates were mean-centred, intercept terms represent model expectations when all covariates are held to their average value. Information on the mean, SD and range of continuous covariates is provided in Table 1. We declared fixed effects statistically significant if their 95% confidence interval did not overlap 0. Confidence intervals were generated using parametric bootstrapping ( $N = 999$ ). To assess the biological significance of significant effects detected in this model, we calculated how model predictions would vary in response to changes in values of predictor variables.

## RESULTS

More than half of all experimental seedlings died during the first 3 years of the study, with one-third (33.5%) of the original 560 individuals surviving to our final (6 year) census point in 2014 (Fig. 2A). Likewise, plant height increased rapidly during the first 3 years, but then levelled off (Fig. 2B); average ( $\pm$  SD) height for seedlings that survived until 2014 was  $1.22 \pm 0.46$  m (range: 0.34–2.42 m). In contrast, the average number of leaves per seedling did not vary strongly during the study; the average number of leaves ( $\pm$  SD) for seedlings that survived until 2014 was  $3.26 \pm 1.26$  (range: 1–6) (Fig. 2C).

### LEK VS. CONTROL

The number of seedlings and juveniles within 5 m of experimental seedlings was almost twice as high in lek sites compared with control sites (mean  $\pm$  SD; lek:  $11.8 \pm 15.0$ , control:  $6.3 \pm 18.6$ ); adult density did not vary (Table 2). Despite this dramatic difference in conspecific density, survival, height and number of leaves of experimental seedlings were not significantly different in lek sites compared with control sites (Table 3, Fig. 3). Leks did not differ from control sites in any measured habitat characteristic, including light availability (Table 2).

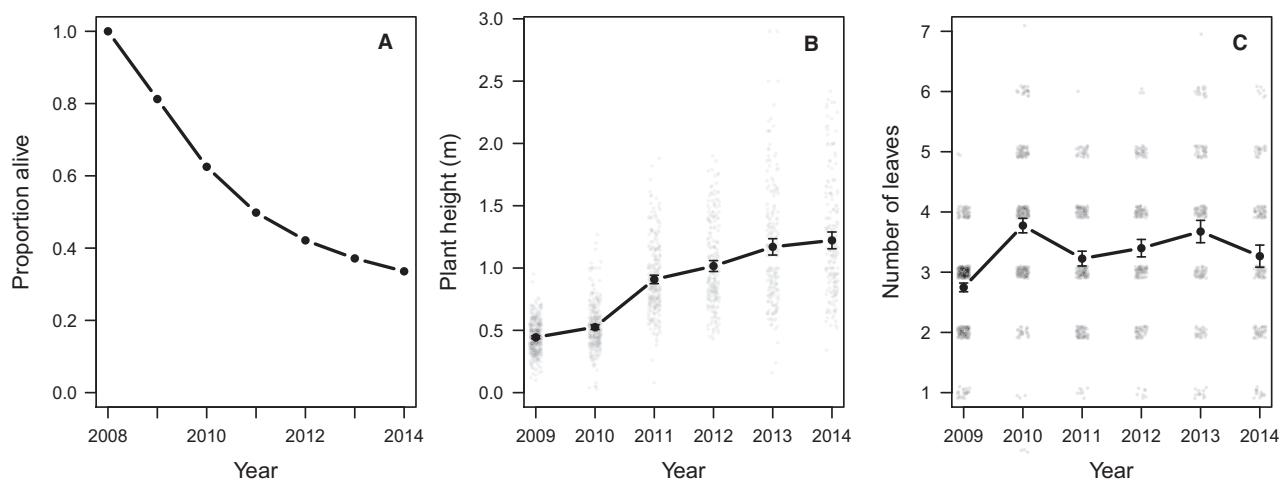
### RELATEDNESS

Seedlings with related neighbours were significantly smaller than seedlings surrounded by unrelated neighbours (Table 3, Fig. 3). There was no relationship between survival or number of leaves and our measure of relatedness (Table 3, Fig. 3).

**Table 1.** Descriptive statistics for continuous covariates used in survival and growth models

	Survival model				Growth models (height and no. of leaves)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Lek vs. non-lek	0.5	0.5	0	1	0.62	0.49	0	1
Related vs. non-related	0.5	0.5	0	1	0.51	0.5	0	1
Elevation (m)	517.21	49.28	407	640	521.79	55.99	407	640
Canopy height (m)	26.26	7.42	9	43	24.85	7.02	15	42
Canopy cover (%)	93.18	3.98	78.94	98.44	91.96	4.82	78.94	98.44
Adult within 5 m	0.06	0.23	0	1	0.06	0.24	0	1
Trees with dbh > 50 cm	0.3	0.46	0	1	0.17	0.38	0	1
Seedling and juveniles within 5 m	9.07	17.12	0	78	8.39	16.67	0	78

Presented are the mean, standard deviation (SD) and minimum and maximum values. Note that the number of plots between the survival ( $N = 70$ ) and growth models ( $N = 53$ ) differs because there were 17 plots in which no seedlings survived to the end of the study period.



**Figure 2.** Survival and growth of *Oenocarpus bataua* seedlings in north-western Ecuador over a 6-year period. A, proportion of individuals surviving; B, plant height among surviving individuals (m); and C, number of leaves among surviving individuals for each annual census point from initial planting in 2008 to final census in 2014. For B and C, filled black circles are average values, error bars represent 1 SE, and light grey circles are observed values, jittered to reduce overlap.

**Table 2.** Regression coefficients from generalized linear mixed models comparing microhabitat and conspecific neighbour characteristics between leks of the long-wattled umbrellabird and control sites in north-western Ecuador

	Intercept	Est.	SE	2.5%	97.5%
Elevation (m)	502.94	28.540	26.64	-21.967	81.526
Canopy height (m)	27.318	-2.118	2.794	-7.434	3.026
Canopy cover (%)	93.884	-1.402	1.571	-4.512	1.835
Adults within 5 m	-4.109	1.193	1.417	-60.370	35.975
Trees > 50 cm dbh	-0.561	-0.727	0.617	-2.131	0.436
Seedling and juveniles within 5 m	<b>-1.182</b>	<b>2.77</b>	<b>1.23</b>	<b>0.840</b>	<b>5.547</b>

Each row represents a separate model, with lek vs. non-lek as a binary predictor and the microhabitat and conspecific neighbourhood characteristic in the first column as the response variable. Seedlings and juveniles within 5 m was modelled using a Poisson error structure. Adults within 5 m and trees > 50 cm dbh was modelled with a binomial error structure. All other characteristics were modelled using a standard linear mixed model with a Gaussian error structure. The intercept represents the estimated value in control sites. Note that estimates for adults within 5 m and trees > 50 cm dbh are on the logit scale, whereas the estimate for seedling and juveniles within 5 m is on the log scale. Est = estimated coefficient, which represents the estimated difference between control sites and lek sites; SE = standard error of the difference between control sites and lek sites; 2.5% is the lower confidence interval estimate and 97.5% is the upper confidence interval estimate calculated from parametric bootstraps ( $N = 999$ ) of the difference between control sites and lek sites; statistically significant results where the confidence interval does not cross 0 are indicated in bold type.

#### CONSPECIFIC DENSITY

The number of conspecific seedlings and juveniles within 5 m of experimental seedlings was associated with fewer leaves at the final census point, but not with a decrease in survival or height (Table 3, Fig. 4). The number of adults within 5 m was not associated with reduced survival or growth (Table 3, Fig. 3). The relationship between conspecific density and growth in terms of number of leaves was robust

to removing outlier plots with > 40 seedlings and juveniles (Supporting Information, Table S1).

#### MICROHABITAT

Canopy cover, our primary measure of light availability, was significantly associated with decreased seedling survival, height and number of leaves (Table 3, Fig. 4). Survival and total number of

**Table 3.** Standardized regression coefficients from a generalized linear mixed model evaluating the relative impact of various parameters on survival, height and number of leaves in experimentally planted seedlings of the canopy palm *Oenocarpus bataua* in north-western Ecuador

	Survival			Height			No. of leaves					
	Est.	SE	2.5%	97.5%	Est.	SE	2.5%	97.5%	Est.	SE	2.5%	97.5%
Intercept	-0.962	0.354	-1.655	-0.28	1.153	0.056	1.033	1.254	1.162	0.041	1.064	1.227
Lek vs. non-lek	0.634	0.706	-0.745	2.154	-0.13	0.106	-0.358	0.075	-0.116	0.099	-0.315	0.08
Related vs. non-related	0.042	0.223	-0.404	0.478	-0.086	0.043	-0.178	-0.003	-0.039	0.082	-0.203	0.13
Elevation	-0.003	0.68	-1.401	1.399	0.188	0.122	-0.058	0.449	-0.1	0.101	-0.307	0.092
Canopy height	0.082	0.441	-0.78	1.017	-0.017	0.109	-0.266	0.205	0.1	0.096	-0.103	0.284
Canopy cover	-1.444	0.452	-2.503	-0.607	-0.366	0.112	-0.584	-0.142	-0.275	0.086	-0.435	-0.102
Adult within 5 m	0.04	0.378	-0.766	0.798	0.04	0.096	-0.163	0.225	-0.034	0.089	-0.22	0.135
Tree > 50 cm dbh	-1.347	0.42	-2.211	-0.557	-0.136	0.092	-0.32	0.042	-0.219	0.096	-0.428	-0.048
Seedling + juvenile density	0.315	0.449	-0.956	1.281	-0.171	0.092	-0.357	0.016	-0.221	0.099	-0.423	-0.041

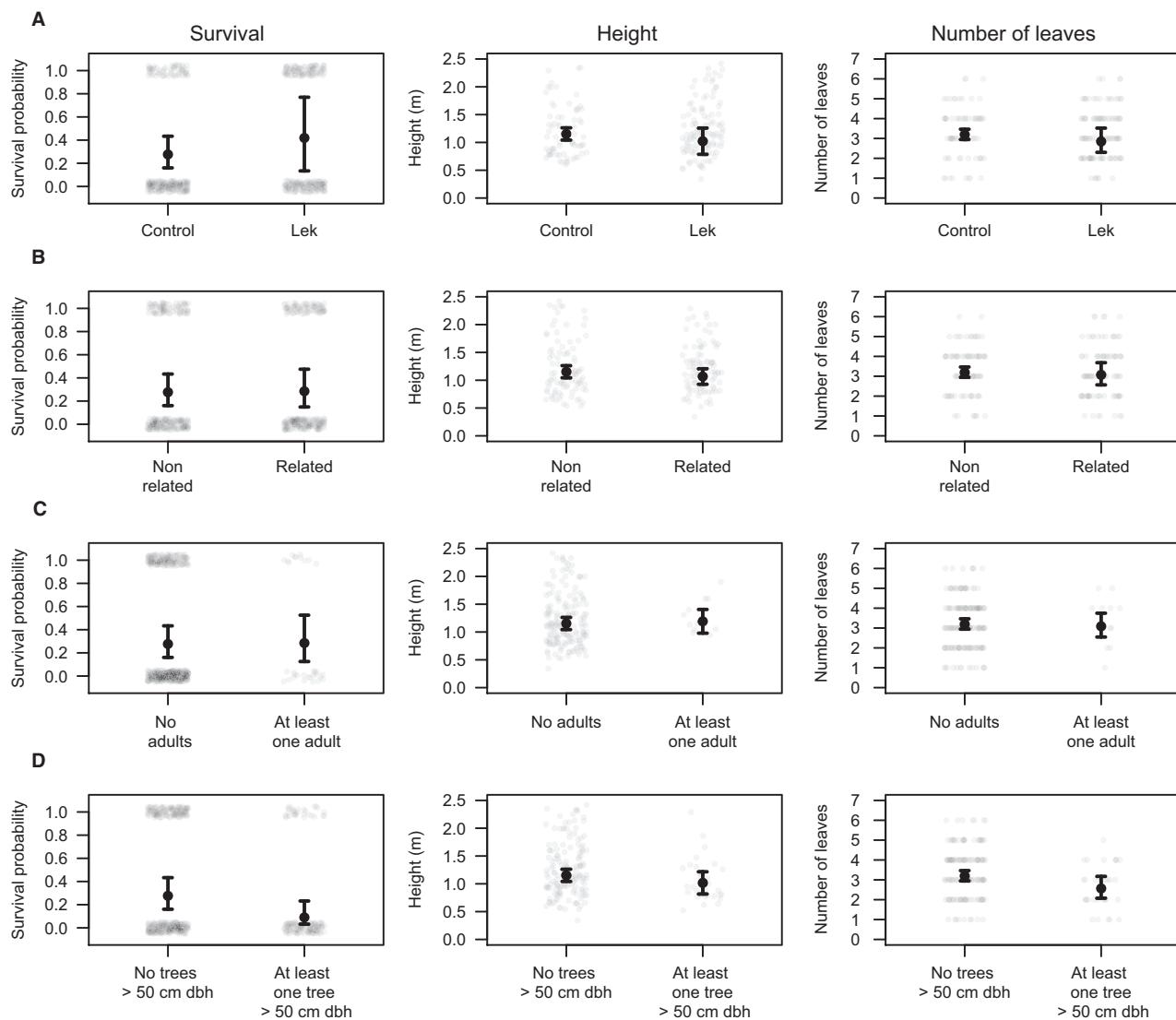
Est = estimated coefficient, SE = standard error, 2.5% is the lower confidence interval estimate and 97.5% is the upper confidence interval estimate calculated from parametric bootstraps ( $N = 999$ ); statistically significant results where the confidence interval does not cross 0 are indicated in bold type. Covariates were mean-centred and scaled by dividing by 2 SD prior to analysis (see Table 1, for information on mean values and SD of covariates).

leaves, but not height, were also lower in areas that had higher densities of trees > 50 cm dbh (Table 3, Fig. 3); this pattern was robust to outliers (see Supporting Information, Table S2). Elevation and canopy height did not have a significant effect on survival or growth (Table 3).

## DISCUSSION

In this experimental study we assessed the relative importance of microhabitat, conspecific density and relatedness on survival and growth of seedlings of the widespread Neotropical palm *O. bataua*. As with many studies on palms and other rainforest plants, light levels explained most of the variance in seedling performance: increased survival and growth were associated with decreased canopy cover and fewer large trees. Corroborating correlative results of an earlier study (Karubian *et al.*, 2012), there was no evidence for reduced seedling survival in lek sites of a key dispersal agent, the long-wattled umbrellabird, despite a markedly higher density of conspecific seedlings and juveniles in these sites. In addition to high seed and seedling density, umbrellabird leks are also characterized by high maternal seed and seedling source diversity (Karubian *et al.*, 2010; Scofield *et al.*, 2012). Our experiment demonstrated that although relatedness of neighbouring experimental seedlings had no discernible impact on survival, it did negatively affect plant height. These findings shed light on the relative importance of various processes that underlie seedling survival and performance, provide insights into the degree to which NDD mechanisms may operate away from source trees and underline the importance that behavioural ecology of animal seed dispersal agents can have on plant demography.

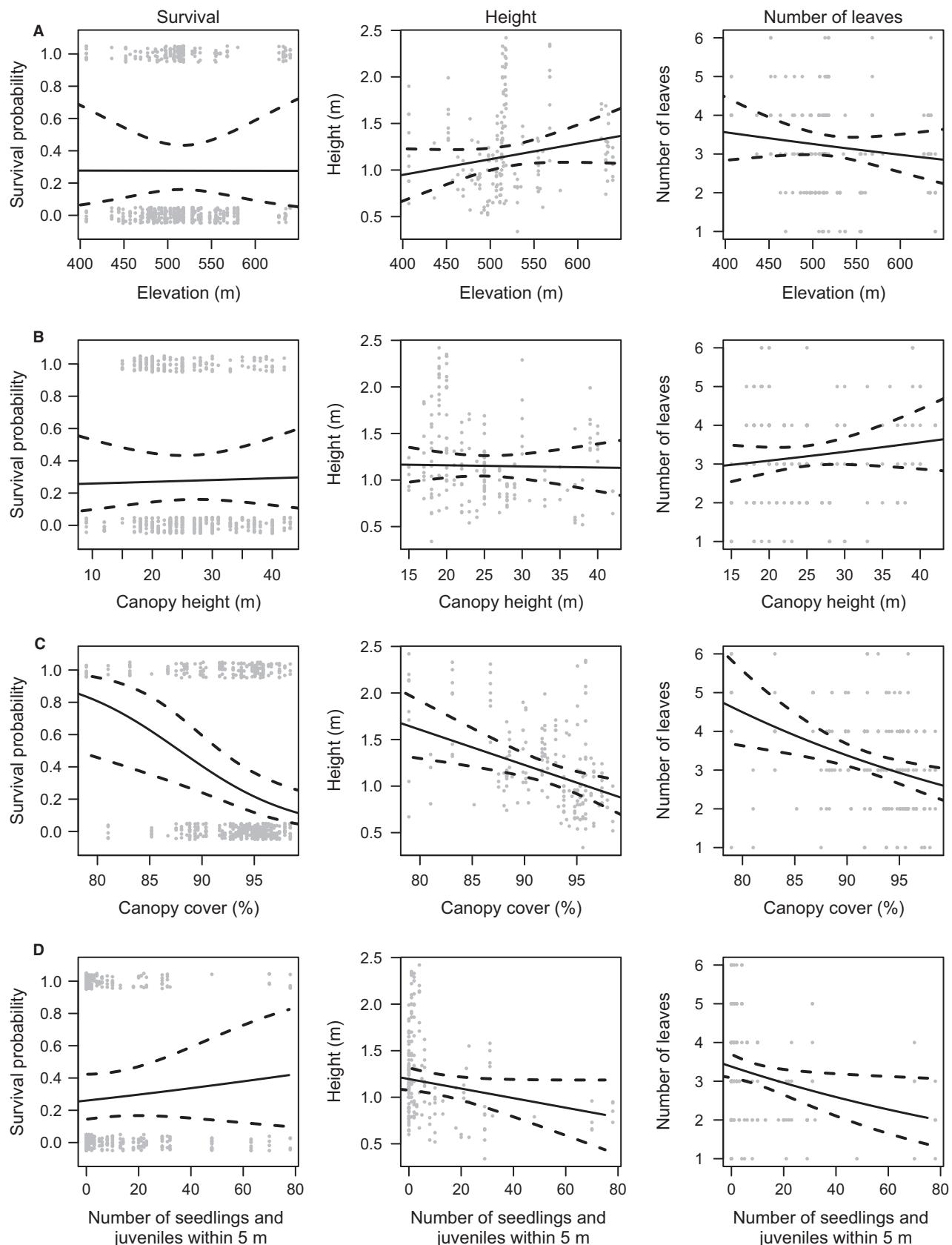
There is overwhelming support for NDD mortality being a strong driver of seedling demography near source trees, but less is known about how these processes operate at high-density sites away from source trees (Comita *et al.*, 2014). This represents a considerable knowledge gap because most if not all animal dispersal agents produce non-random deposition patterns characterized by high seed and seedling densities at certain locations away from source trees (Karubian & Durães, 2009; Cortes & Uriarte, 2013). Other studies assessing NDD away from source trees report mixed results: high-density sites away from source trees are associated with relatively high survival in some systems (Muñoz Lazo *et al.*, 2011; Sica, Bravo & Giombini, 2014) and relatively low survival in others (Kitamura *et al.*, 2004; Russo & Augspurger, 2004), suggesting that patterns may be context specific. Our earlier work on the *O. bataua*



**Figure 3.** Survival and growth of *Oenocarpus bataua* seedlings in north-western Ecuador in relation to location and relatedness. A, effect of location in a long-wattled umbrellabird lek vs. randomly selected control site outside the lek on survival, height and number of leaves; there was no significant impact on any of these measures of seedling performance. B, differences between related and unrelated seedlings; increased relatedness with neighbouring seedlings was associated with reduced plant height, but not survival or growth. C, effect of having at least one adult within a 5-m radius. D, the effect of having at least one large tree ( $> 50$  cm dbh) within a 10-m radius. Having at least one large tree was linked to lower survival and fewer leaves. For all plots, filled black circles show predicted mean value with error bars depicting the approximate 95% confidence interval. Light grey circles show observed values, jittered to reduce overlap (see Table 3 for details on statistical analyses).

umbrellabird study system used a correlational approach to infer that there was no reduction in the probability of transition from seed to seedling in umbrellabird leks, despite higher densities at these sites (Karubian *et al.*, 2012). The current project confirms higher seedling densities in leks and shows that there is no measurable impact on seedling survival or height at these sites. We did observe a significant, negative relationship between density and

leaf number, but question the biological significance of this finding for three reasons. First, because leaf number does not increase with age (Fig. 2C), the utility of this trait as an index of plant performance is unclear. Second, the effect was relatively weak: a large increase (33.34) in the number of seedlings and juveniles within 5 m of a plot yields a predicted reduction of 0.80 leaves, or 24% of the average number of leaves per individual (Table 3). Third, because



**Figure 4.** Survival and growth of *Oenocarpus bataua* seedlings in north-western Ecuador in relation to habitat characteristics and conspecific neighbourhood: A, elevation; B, canopy height; C, canopy cover; and D, number of conspecific seedlings and juveniles within 5 m. Increased canopy cover (C) reduced all measures of seedling performance. Solid black line shows model predictions, with dashed line showing 95% confidence intervals. Light grey circles are observed values, with values jittered around 0 and 1 on survival graphs to reduce overlap (see Table 3 for details on statistical analyses).

slope is correlated with seedling and juvenile density in this system (see Methods), it may be that slope is responsible for the decrease in growth rates, rather than seedling and juvenile density per se; the current study was not able to disentangle these two effects due to correlations between these variables. Given that different selection pressures play out at the seed vs. seedling stage (e.g. Fricke, Tewksbury & Rogers, 2014), we may have obtained different results if we sowed seeds rather than germinated seedlings in this study, suggesting one potential avenue for future research.

Why did we fail to document reduced seedling survival in lek sites, as might be expected given higher densities? We can rule out a beneficial effect of gut passage by umbrellabirds (e.g. Fricke *et al.*, 2013), because seeds used in this study did not pass through umbrellabird guts. An alternative possibility is that microhabitat differences between leks and control areas may somehow compensate for any negative effects of higher densities in leks by providing favourable conditions for seedlings at these sites. The strongest predictor of survival and growth among the variables we measured was access to light. The biological significance of these effects appears to be substantial in this system. For example, increasing canopy cover from 85 to 100% led to a predicted 37.6% decrease in seedling survival, and a 9.64% increase in canopy cover led to a predicted height reduction of 36.6 cm, or 30%, of an average plant. Similarly, addition of at least one large tree within 5 m of seedlings led to a predicted 25.2% decrease in survival; the effect on seedling height was also negative although the relationship was not significant. We note that the effect of canopy coverage on seedling height may not be independent from survival; that is, because taller seedlings are expected to have higher survival rates (e.g. Queenborough *et al.*, 2007), shorter seedlings are probably those that die. Leaf number also responded negatively to increased canopy cover (a 9.65% increase in cover led to a predicted decrease of 0.759 leaves, or 23.2%) and presence of a large tree (predicted decrease of 0.803 leaves, or 24.6%), although the uncertainty around how to interpret this variable in this system (above) draws into question the biological significance of these leaf number findings.

Light as a limiting factor for seedling growth is a common pattern among rainforest plants because the floor of closed-canopy forests often receives only a small fraction (< 2%) of available photosynthetic energy (Augspurger, 1984; Chazdon *et al.*, 1996; Queenborough *et al.*, 2007). As ubiquitous components of tropical forests, it is perhaps not surprising that most rainforest palms appear to follow this pattern (e.g. Svenning, 2002; dos Santos *et al.*, 2012). However, there was no significant difference between leks and control sites in light levels, suggesting that other factors not measured in this study could contribute in substantive ways to survival of seedlings in lek and control sites, despite higher densities in leks. In particular, and as is the case in many other palms (Eiserhardt *et al.*, 2011; Andersen *et al.*, 2014), it may be that soil characteristics play an important role in determining survival and growth. We might expect soil characteristics to vary between leks and control sites because umbrellabird leks are frequently located in a distinctive topographical area (i.e. ridge tops, our unpubl. data). It is also possible that umbrellabirds enhance soil conditions for seedlings via regular defecation at these traditionally used display sites. A future study measuring soil characteristics (including hydrology) would help to provide resolution among these alternatives.

Alternatively, it may be that lower levels of relatedness among naturally occurring (i.e. non-experimental) seedlings in lek sites might have acted to weaken the impact of NDD processes on experimental seedlings in leks relative to those planted in control sites. Currently, little is known about how degree of intraspecific relatedness impacts growth and survival of tropical plants in natural contexts and what the mechanisms driving these outcomes may be. We hypothesized three ways in which degree of relatedness, either among our experimental seedlings or via effects of non-experimental seedlings on our experimental seedlings, might influence the outcome of our experiment: (1) increased susceptibility to attack among closely related neighbouring individuals might have a negative effect; (2) kin selection among closely related neighbouring individuals might lead to a competitive advantage; and (3) increased competition via greater niche overlap among closely related individuals might have a negative effect. There was no difference in plant survival

or growth in leks and outside leks, suggesting that any (unmeasured) differences that may have existed in the relatedness of non-experimental seedlings in these two contexts did not have a detectable impact on experimental seedlings.

We found, however, that relatedness had a weak but statistically significant negative impact on seedling growth (but not survival). Seedlings were on average 0.09 m taller when surrounded by unrelated neighbours vs. related neighbours, which corresponds to a c. 7% difference relative to average plant height. We consider this difference to be biologically significant given the intense competition among seedlings for access to light, such that relatively modest differences in height may therefore influence survival (e.g. Queenborough *et al.*, 2007). These findings provide tentative support for the idea that competition that limits resources among more closely related individuals (in this case experimental seedlings planted in close proximity) may impair performance, corroborating similar results from other recent studies (e.g. Milla *et al.*, 2009; Cheplick & Kane, 2010). However, more work is needed to reach confident conclusions on this question. Future studies might move beyond the relatively crude, but clear-cut, categorical measure of relatedness we employed in the current study (i.e. sibs and half-sibs collected from the same infructescences vs. individuals collected from different trees) to assess how continuous measures of genetic diversity (e.g. heterozygosity, inbreeding, allelic richness) or genetic uniqueness relative to other conspecifics may influence seed and seedling performance (e.g. Liu *et al.*, 2015).

The current study provides two, distinct pieces of information that are consistent with the idea that lek-breeding male umbrellabirds provide directed dispersal that promotes survival among seedlings of *O. bataua*. First, we experimentally confirm that *O. bataua* recruitment in leks is equivalent to control sites, despite higher densities of seeds and seedlings in these sites, suggesting that some factor may enhance seedling survival at these sites (i.e. to counter-balance expected NDD effects). Second, lower relatedness was associated with increased plant height, and umbrellabirds are known to produce highly diverse seed pools in leks, suggesting a potential additional advantage to dispersal by umbrellabirds. Like many large-bodied frugivores, umbrellabirds are at risk of extinction and the consequences of disruption to the dispersal mutualism between umbrellabirds and *O. bataua* remain unknown. It seems likely that umbrellabird extinction might lead to reduced recruitment and increased genetic relatedness among *O. bataua* seedlings. Consistent with this prediction, Browne, Ottewell &

Karubian (2015) found higher genetic relatedness among *O. bataua* seedlings in forest fragments where umbrellabirds are locally extinct compared with continuous forest with healthy populations of umbrellabirds, citing the lack of umbrellabirds as a potential cause. Understanding the possible consequences of defauna for plant population dynamics remains a topic of global interest and importance; linking frugivore behaviour with processes driving plant recruitment will be a critical step in achieving this goal.

## ACKNOWLEDGEMENTS

We gratefully acknowledge the support of FCAT (Fundación para la Conservación de los Andes Tropicales), the Jatun Sacha Foundation, local residents and landowners of the Mache-Chindul reserve and the Ecuadorian Ministry of the Environment. Valuable assistance and support was provided by C. Aulestia, J. Bermingham, F. Castillo, J. B. Cox, A. Ruohomäki and M. Gonzalez. This project was supported by the Conservation, Food & Health Foundation, Disney Conservation Fund, National Science Foundation (EAGER no. 1548548, DDIG no. 1501514 and a Graduate Research Fellowship to L.B.), Tulane University and the United States Fish & Wildlife Service (NMBCA no. 5605). All research was conducted with approval of the Ecuadorian Ministry of the Environment (Permit 010-2015-IC-FLO-FAU-DPE-MA).

## REFERENCES

- Alvarez-Loayza P, Terborgh J.** 2011. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? *Journal of Ecology* **99**: 1045–1054.
- Andersen KM, Turner BL, Dalling JW.** 2014. Seedling performance trade-offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology* **95**: 3399–3413.
- Augspurger CK.** 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* **72**: 777.
- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT.** 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**: 85–88.
- Bates D, Maechler M, Bolker B, Walker S.** 2015. *lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-9*. Available at: <https://cran.r-project.org/package=lme4>
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS.** 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127–135.

- Browne L, Ottewell K, Karubian J.** 2015. Short-term genetic consequences of habitat loss and fragmentation for the Neotropical palm *Oenocarpus bataua*. *Heredity* **115**: 385–395.
- Carrasco L, Berg KS, Litz J, Cook A, Karubian J.** 2013. Avifauna of the Mache Chindul Ecological Reserve, northwest Ecuador. *Ornitologia Neotropical* **24**: 321–334.
- Chazdon RL, Pearcy RW, Lee DW, Fetcher N.** 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey SS, Chazdon RL, Smith AP, eds. *Tropical forest plant ecophysiology*. New York: Chapman & Hall, 5–55.
- Cheplick GP, Kane KH.** 2010. Genetic relatedness and competition in *Triplasis purpurea* (Poaceae): resource partitioning or kin selection? *International Journal of Plant Sciences* **165**: 623–630.
- Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP.** 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* **329**: 330–332.
- Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, Zhu Y.** 2014. Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* **102**: 845–856.
- Cortes MC, Uriarte M.** 2013. Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biological Reviews* **88**: 255–272.
- Eiserhardt WL, Svensson JC, Kissling WD, Balslev H.** 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany* **108**: 1391–1416.
- File AL, Murphy GP, Dudley SA.** 2012. Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the Royal Society B* **279**: 209–218.
- Fricke EC, Simon MJ, Reagan KM, Levey DJ, Riffell JA, Carlo TA, Tewksbury JJ.** 2013. When condition trumps location: seed consumption by fruit-eating birds removes pathogens and predator attractants. *Ecology Letters* **16**: 1031–1036.
- Fricke EC, Tewksbury JJ, Rogers HS.** 2014. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecology Letters* **17**: 593–598.
- Garcia C, Grivet D.** 2011. Molecular insights into seed dispersal mutualisms driving plant population recruitment. *Acta Oecologica* **37**: 632–640.
- Gelman A.** 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* **27**: 2865–2873.
- Gentry AH.** 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* **63**: 19–28.
- Grivet D, Smouse PE, Sork VL.** 2005. A novel approach to an old problem: tracking dispersed seeds. *Molecular Ecology* **14**: 3585–3595.
- Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA.** 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**: 493–495.
- Howe HF.** 1989. Scatter-dispersal and clump-dispersal and seedling demography – hypothesis and implications. *Oecologia* **79**: 417–426.
- Howe HF, Smallwood J.** 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**: 201–228.
- IUCN.** 2015. *Red List of Threatened Species. Version 2015.2*. *Cephalopterus penduliger*. Available at: [www.iucnredlist.org](http://www.iucnredlist.org)
- Janzen DH.** 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501–528.
- Jongsma GFM, Hedley RW, Durães R, Karubian J.** 2014. Amphibian diversity and species composition in relation to habitat type and alteration in the Mache-Chindul Reserve, northwest Ecuador. *Herpetologica* **70**: 34–46.
- Jordano P, Garcia C, Godoy JA, Garcia-Castano JL.** 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 3278–3282.
- Karubian J, Durães R.** 2009. Effects of seed disperser social behavior on patterns of seed movement and deposition. *Oecologia Brasiliensis* **13**: 45–57.
- Karubian J, Durães R.** 2014. Impacts of mating behaviour on plant-animal seed dispersal mutualisms: a case study from a Neotropical lek-breeding bird. In: Maceido R, Machado G, eds. *Sexual selection: insights from the Neotropics*. Amsterdam: Elsevier, 365–390.
- Karubian J, Durães R, Storey JL, Smith TB.** 2012. Mating behaviour drives seed dispersal by the long-wattled umbrellabird *Cephalopterus penduliger*. *Biotropica* **44**: 689–698.
- Karubian J, Ottewell K, Link A, Di Fiore A.** 2015. Genetic consequences of seed dispersal to sleeping trees by white-bellied spider monkeys. *Acta Oecologica* **68**: 50–58.
- Karubian J, Sork VL, Roorda T, Durães R, Smith TB.** 2010. Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology* **19**: 1745–1753.
- Kitamura S, Yumoto T, Poonswad P, Noma N, Chuailua P, Plongmai K, Maruhashi T, Suckasam C.** 2004. Pattern and impact of hornbill seed dispersal at nest trees in a moist evergreen forest in Thailand. *Journal of Tropical Ecology* **20**: 545–553.
- Liu X, Etienne RS, Liang M, Wang Y, Yu S.** 2015. Experimental evidence for an intraspecific Janzen–Connell effect mediated by soil biota. *Ecology* **96**: 662–671.
- Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, Sanchez EI, Bever JD.** 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**: 752–755.
- Milla R, Forero DM, Escudero A, Iriondo JM.** 2009. Growing with siblings: a common ground for cooperation or for fiercer competition among plants? *Proceedings of the Royal Society B* **276**: 2531–2540.
- Munoz Lazo FJJ, Culot L, Huynen MC, Heymann EW.** 2011. Effect of resting patterns of tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) on the spatial distribution of seeds and seedling recruitment. *International Journal of Primatology* **32**: 223–237.

- Nathan R, Muller-Landau HC.** 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**: 278–285.
- Ortega-Andrade HM, Bermingham J, Aulestia C, Pau-car C.** 2010. Herpetofauna of the Bilsa Biological Station. *Checklist* **6**: 119–154.
- Ottewell K, Grey E, Castillo F, Karubian J.** 2012. The pollen dispersal kernel and mating system of an insect-pollinated tropical palm, *Oenocarpus bataua*. *Heredity* **109**: 332–339.
- Queenborough SA, Burslem DFRP, Garwood NC, Valencia R.** 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology* **88**: 2248–2258.
- Rodriguez-Perez J, Traveset A.** 2007. A multi-scale approach in the study of plant regeneration: finding bottlenecks is not enough. *Perspectives in Plant Ecology Evolution and Systematics* **9**: 1–13.
- Russo SE, Augspurger CK.** 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters* **7**: 1058–1067.
- dos Santos MLS, Franca S, Gomes FP, do Nascimento JL, dos Anjos Silva L, Mielke MS** 2012. Low light availability affects leaf gas exchange, growth and survival of *Euterpe edulis* seedlings transplanted into the understory of an anthropic tropical rainforest. *Southern Forests* **74**: 167–174.
- Schielzeth H.** 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* **1**: 103–113.
- Schupp EW, Fuentes M.** 1995. Spatial patterns of seed dispersal and the unification of plant-population ecology. *Eco-science* **2**: 267–275.
- Schupp EW, Jordano P, Maria GJ.** 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* **188**: 333–353.
- Scofield DG, Smouse PE, Karubian J, Sork VL.** 2012. Use of alpha, beta, and gamma diversity measures to characterize seed dispersal by animals. *American Naturalist* **180**: 719–732.
- Sica YV, Bravo SP, Giombini MI.** 2014. Spatial pattern of Pindó palm (*Syagrus romanzoffiana*) recruitment in Argentinian Atlantic Forest: the importance of tapir and effects of defaunation. *Biotropica* **46**: 696–703.
- Spiegel O, Nathan R.** 2010. Incorporating density dependence into the directed-dispersal hypothesis. *Ecology* **91**: 1538–1548.
- ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino JF, Monteagudo A, Vargas PN, Montero JC, Feldpausch TR, Coronado ENH, Killeen TJ, Mostacedo B, Vasquez R, Assis RL, Terborgh J, Wittmann F, Andrade A, Laurance WF, Laurance SGW, Marimon BS, Marimon BH Jr, Vieira ICG, Amaral IL, Brienen R, Castellanos H, López DC, Duivenvoorden JF, Mogollón HF, de Almeida MF, Dávila N, García-Vilacorta R, Diaz PRS, Costa F, Emilio T, Levis C, Schiatti J, Souza P, Alonso A, Dallmeier F, Montoya AJD, Piedade MTF, Araujo-Murakami A, Arroyo L, Gribel R, Fine PVA, Peres CA, Toledo M, Aymard CGA, Baker TR, Cerón C, Engel J, Henkel TW, Maas P, Petronelli P, Stropp J, Zartman CE, Daly D, Neill D, Silveira M, Paredes MR, Chave J, de Andrade LFD, Jørgensen PM, Fuentes A, Schöngart J, Valverde FC, Di FA, Jimenez EM, Mora MCP, Phillips JF, Rivas G, van Andel TR, von Hildebrand P, Hoffman B, Zent EL, Malhi Y, Prieto A, Rudas A, Ruschell AR, Silva N, Vos V, Zent S, Oliveira AA, Schutz AC, Gonzales T, Nascimento MT, Ramirez-Angulo H, SIERRA R, Tirado M, Medina MNU, der van Heijden G, Vela CIA, Torre EV, Vriesendorp C, Wang O, Young KR, Baider C, Balslev H, Ferreira C, Mesones I, Torres-Lezama A, Giraldo LEU, Zagt R, Alexiades MN, Hernandez L, Huamantupa-Chuquimaco I, Milliken W, Cuenca WP, Paulette D, Sandoval EV, Gamarra LV, Dexter KG, Feeley K, Lopez-Gonzalez G, Silman MR.** 2013. Hyperdominance in the Amazonian tree flora. *Science* **342**: 1243092.
- Svenning JC.** 2002. Crown illumination limits the population growth rate of a Neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). *Plant Ecology* **159**: 185–199.
- Terborgh J.** 2012. Enemies maintain hyperdiverse tropical forests. *American Naturalist* **179**: 303–314.
- Wang BC, Smith TB.** 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**: 379–385.
- Wenny DG, Levey DJ.** 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* **95**: 6204–6207.
- Zuur AF, Ieno EN, Elphick CS.** 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**: 3–14.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Standardized regression coefficients from a generalized linear mixed model after removing plots with > 40 seedlings and juveniles in a 5-m radius.

**Table S2.** To test whether negative associations of survival and growth with canopy cover were robust to potential outliers, we re-ran analyses excluding plots with < 86% canopy cover (this value was chosen because only seven plots had < 86% canopy cover).