How many seeds does it take to make a sapling?

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Abstract. Tall canopy trees produce many more seeds than do understory treelets, yet, on average, both classes of trees achieve the same lifetime fitness. Using concurrent data on seedfall (8 years) and sapling recruitment (12 years) from a long-established tree plot at the Cocha Cashu Biological Station in Perú, we show, that a 40-m canopy tree must produce roughly 13 times the mass of seeds to generate a sapling as a 5-m tall understory treelet. Mature tree height accounted for 41% of the variance in *seed mass* per sapling recruit in a simple univariate regression, whereas a multivariate model that included both intrinsic (seed mass, tree height, and dispersal mode) and extrinsic factors (sapling mortality as a surrogate for microsite quality) explained only 31% of the variance in *number of seeds* per sapling recruit. The multivariate model accounted for less variance because tall trees produce heavier seeds, on average, than treelets. We used "intact" (mostly dispersed) seeds to parameterize the response variable so as to reduce, if not eliminate, any contribution of conspecific crowding to the difference in reproductive efficiency between canopy trees and treelets. Accordingly, a test for negative density dependence failed to expose a relationship between density of reproductive trees in the population and reproductive efficiency (seed mass per recruit). We conclude that understory treelets, some of which produce only a dozen seeds a year, gain their per-seed advantage by failing to attract enemies à la Janzen-Connell, either in ecological or evolutionary time.

Key words: Amazonia; Janzen-Connell hypothesis; Perú; sapling mortality; sapling recruitment; seed dispersal; seed mass; structural equation modeling; tree height; tropical forest.

INTRODUCTION

How many seeds does it take to make a sapling? The question seems deceptively simple, but has been little investigated. The question is of interest from both theoretical and practical standpoints. On the theoretical side, it is of interest to test the null hypothesis that a seed is a seed is a seed (once adjusted for seed mass and other relevant factors). If species were found to differ substantially in the number (or mass) of seeds required to generate a sapling, after accounting for confounding variables, it would imply that the factors regulating sapling recruitment differ across species. Such factors might consist of varying seedling light requirements, differing dispersal success, competitive ability or susceptibility to pests and pathogens. On the practical side, the results could suggest levels of seed augmentation that might be required to enhance the recruitment of desired species.

Previous investigators have found that reproductive efficiency varies inversely with tree height. King et al. (2006), using data from 70 tree species on Barro Colorado Island, Panama, found that survival of seeds and seedlings was greater for understory treelets than for trees of canopy stature. Kohyama et al. (2003) came to a similar conclusion from data on the recruitment of 27 species in a Bornean dipterocarp forest. But what is the reason for small-tree reproductive advantage? This is the question we pursue herein.

To begin, some background will be helpful. Tropical forests are often seed starved (seed limitation, Nathan and Muller-Landau 2000). Seed augmentation experiments typically yield positive results for many species—more seeds in, more seedlings out. This important fact has been demonstrated repeatedly in tropical forests on different continents

(Svenning and Wright 2005; reviewed by Clark et al. 2007). However, some tree species produce a copious seedfall, yet generate few saplings. Such species tend to respond weakly to seed augmentation and are considered to be establishment limited (Nathan and Muller-Landau 2000, Norghauer and Newbery 2010, Muscarella et al. 2012). At our research site, the Cocha Cashu Biological Station in Amazonian Peru, the rain of dispersed seeds of 30 common trees that are regular as saplings is $<1/\text{m}^2$-yr for every species, suggesting widespread seed limitation (Terborgh et al. 2011). Accordingly, the density of tree seedlings is low, $\sim 5/\ \text{m}^2$ (Harms et al. 2004) and the density of all plants <30 cm tall sums to $\sim 20/\text{m}^2$ (tree and liana seedlings and herbs; Terborgh and Wright 1994). These densities lie far below the threshold of ~100 plants/m^2 at which strong seedling competition becomes apparent (Weiner 1995, Terborgh et al. 2002, Wright 2002). The small saplings we shall later be considering occur in the plot at a mean density of $\sim 0.5/\text{m}^2$, again, a value too low to generate strong intracohort effects (Paine et al. 2008, Terborgh 2012). Thus, limitations of seed input, invoking the winner by forfeit paradigm, appear to be widespread in the forest at Cocha Cashu (Hurt and Pacala 1995, Muller-Landeau et al. 2008, Terborgh et al. 2011).

It can be suspected that the seeds of different tree species will possess greatly differing survival prospects because reproductive effort per seed-bearing adult, defined for our purposes as:

(number of seeds falling per ha-yr) × (mean seed dry mass) / (number of seed-bearing individuals per ha) varies between species by $>10^3$ (Table A1). Yet, at equilibrium, the reproductive efforts of all species are equivalent in that they just suffice to replace the current generation.

To be more concrete, a large canopy tree may produce thousands of seeds a year, whereas an understory treelet may produce only a few dozen. Other things being equal (e.g., seed mass, germination, establishment requirements), a seed of the treelet must have a much greater chance of becoming a sapling than a seed of the canopy tree. Is this true and, if so, why is it true?

Addressing the question in a comparative context requires several types of data for a broad sample of tree species that includes both understory treelets and members of the high canopy. Other things being equal, sapling recruitment will depend on seed and seedling survival and these, in turn, will depend on various factors, including seedfall and the fraction of seeds dispersed, dispersal mode, seed mass, fecundity, and seedling light requirements (or proxies thereof). Gathering each type of data has been a separate project, whereas assembling the entire collection of data sets has been a cumulative process to which many individuals have contributed over a period of more than 20 years.

METHODS

Study site

The research was carried out in a 4-ha tree plot at the Cocha Cashu Biological Station in the Manu National Park, Madre de Dios, Perú (11˚54′ S, 71˚22′ W). The core of the plot where most of the data were collected has been monitored since the 1970s (Gentry and Terborgh 1990) with additions annexed in 1988 and 2002 to bring the total to 4.0 ha. In 1997-1998 we installed a 1.26 ha sapling monitoring subplot centered within the larger tree plot. Since then, all saplings ≥1 m tall and <10 cm dbh (diameter at breast height) have been mapped, measured, and identified at regular 4-yr intervals, with the most recent census having been completed in 2010. To measure concurrent seedfall, we installed a grid of 289 × 0.5 m^2 seed traps overlying the seedling monitoring subplot. The traps were suspended roughly 1 m above the ground, placing them well below the crowns of all species included in the analysis but high enough to avoid disturbance by peccaries and other terrestrial animals. The traps were arrayed at 7.5 m intervals in a square grid covering 1.44 ha and were monitored biweekly for 8.3 years from September 2002 until January 2011 (when funding expired).

Sapling recruitment

Stems within the sapling monitoring subplot were initially tagged, mapped, measured, and identified in two size classes: “small” saplings ≥1 m tall and <1 cm dbh; and “large” saplings ≥1 cm dbh and <10 cm dbh. At each subsequent quadrennial recensus, all stems were remeasured and new stems recruiting into the ≥1 m size class were added to the register. Saplings of the two size classes occurred in the plot at almost identical densities, a mean of 5,022 per ha for small saplings and a mean of 5,020 per ha for large saplings (means of values recorded at the various censuses). Although the area monitored for sapling recruitment was relatively small (1.26 ha), monitoring was continued for 12 years for a total of 11.28 ha-yr between 1998 and 2010. So far as is known, the saplings of all species used in the analyses arise from seed.

Seedfall

Fruits and seeds collected from the traps were sorted to species and classified according to the following categories: “intact” seeds, damaged seeds, seeds with adherent pulp, ripe fruits, unripe fruits, wormy fruits, and a final category for capsules, pods, valves, etc. By definition, “intact” seeds lacked adherent pulp and were normally shiny, as are seeds that have passed through a disperser’s gut. Seeds with adherent dung or seeds associated with dung in the trap were assigned to the intact category. We followed King et al. (2006) in restricting the analysis to species supported by ≥10 intact seeds and ≥10 small sapling recruits.

Dispersed zoochorous seeds are included in the intact category, but not all seeds assigned to this category were dispersed, because intact seeds frequently fall into traps located under fruiting conspecifics. We had previously shown (Terborgh et al. 2002, Terborgh and Nuñez-Ituri 2006, Terborgh et al. 2011) that all or nearly all (>98%) saplings arise from seeds dispersed beyond the projected crowns of fruiting conspecifics and that recruitment of saplings under reproductive conspecifics is essentially nil (Álvarez and Terborgh 2011).

Later, we shall examine sapling recruitment in relation to seedfall represented in two ways. “Gross” seedfall includes all potentially viable seeds (dispersed and undispersed) and is computed as the sum of intact seeds, seeds with adherent pulp and seeds contained in ripe fruits. The second category is that of intact seeds as defined above. We were not able to quantify the seedfall of species with seeds having a long dimension <3-5 mm because the seeds become lost in the jumble of litter and dung in the traps. This limitation excluded three speciose genera with small seeds and several to many species in the local flora (*Ficus*: ≥16 spp., *Miconia*: 4 spp., *Piper*: 7 spp.). *Inga* is another problematic genus we had to exclude because the seeds of its ±20 species overlap greatly in size and cannot reliably be distinguished. Although palms account for roughly a third of the stems ≥10 cm dbh in this forest, we were obliged to neglect them as well because there is no palm counterpart of a 1 m tall dicot sapling to enable an equivalent quantification of recruitment.

Seed mass

Cocha Cashu Biological Station maintains a seed collection containing several hundred taxa and an associated database that includes seed dry mass. The data used were drawn from this database.

Sapling mortality

We calculated mortality as an annualized rate by first using an exponential model to compute a rate, m_i, for the i^{th} sapling cohort:

$$m_i = 1 - \left(1 - \frac{d_i}{n_i}\right)^{1/t_i}$$

in which d_i is the number of stems that died, n_i is the initial number of stems in the cohort, and t_i is the length in years of the corresponding intercensus interval. A species-level mortality, M, was calculated as the cohort mortality (m_i) weighted by the number of stems (n_i):

$$M = \frac{\sum_i n_i m_i}{\sum_i n_i}$$

Tree height

Similarly, Cocha Cashu Biological Station maintains databases of measured tree heights and approximate girth at the onset of reproduction. We chose to use tree height rather than basal area because it is likely to better represent access to the sun, given that subcanopy trees tend to have larger basal areas for a given height than canopy trees (Kohyama et al. 2003, Thompson et al. 2011). Heights were taken from known fruiting adults or from large adults if fruiting individuals had not previously been distinguished. Large adults better represent the average seed source for a species because they tend to be taller and have larger crowns, attributes that can both contribute to enhanced seed production. For species not included in the database, we measured the heights of large individuals with known locations within established tree plots.

Dispersal mode

Species with unique dispersers or even a unique category of disperser (e.g., bird, bat) constitute a minority. Most species of fleshy fruits are potentially dispersed by members of two or more classes of dispersers (birds, primates, etc.), making assignments to simple categories somewhat problematical (Gautier-Hion et al. 1985). While acknowledging these limitations, we followed Terborgh et al. (2008) in assigning species ($N = 48$) to six dispersal modes: autochorous (2 spp.), bat (4 spp.), bird (16 spp.), large primate (12 spp.), small arboreal mammal (12 spp.), and wind (2 spp.).

HYPOTHESES

Our goal is to reveal the factors that contribute to determining how many seeds it takes to make a sapling in each of 48 tree species for which there were ≥10 recruited saplings and ≥10 intact seeds. The number of seeds of a given species falling per ha-yr will depend on the density of reproductive female trees in the population and their aggregate seed production. The per-capita success of seeds can depend on whether the seeds were dispersed or not and on their post-dispersal fates. Seed fates are determined by both intrinsic (seed mass, dispersal mode, establishment requirements) and extrinsic factors that determine survival to the sapling stage. Extrinsic factors are both abiotic (microsite properties) and biotic (exposure to predators, herbivores and pathogens). We used direct measures or proxies for all of the relevant variables except for extrinsic biotic factors influencing survival.

The response variable will be the log of the number of seeds falling per ha-yr per small sapling recruiting per ha-yr (to be termed “seeds per recruit”). Critical to quantifying seeds per recruit is the representation of seedfall, in particular, whether undispersed seeds are included, for, as mentioned above, undispersed seeds rarely produce saplings. The fraction of seeds that are dispersed in the forest at Cocha Cashu varies across species from near zero to 1.0 (Terborgh et al. 2011). Including undispersed seeds in the parameterization of seedfall could thus introduce a major source of uncontrolled variation. Recognizing this, we conducted separate analyses using gross seedfall and the rain of intact seeds.

Parameters used the analysis as explanatory variables or cofactors are included on the basis of *a priori* considerations, as follows.

Seed mass

The ability of seedlings derived from large seeds to tolerate shade, physical damage and herbivory suggests that large-seeded species enjoy greater per-seed success in generating saplings than small-seeded species (e.g., Harms and Dalling 1997; Moles and Westoby 2004). To the extent that this is true in the complex milieu of nature, one would predict a strong negative relationship between seed size and the number of seeds required to generate a sapling.

Sapling mortality

Given that >90% of the forest floor within the sapling monitoring plot lies in the shade of one or more overtopping trees (unpublished results), shade tolerant species can be expected to generate more saplings per seed than sun demanding species. This tendency is obvious, for example, in such light-demanding species as *Ficus* spp. and *Cecropia* spp., that produce huge numbers of tiny seeds that fail to survive, as indicated by an extreme scarcity of saplings of such species. Given that experimentally determining the light response of scores of species of tree seedlings was impractical, we employed a proxy variable, the mortality rate of small saplings to substitute for quality of microsites (cf. Weldon et al. 1991, Hubbell and Foster 1992). Thus we can predict that the number of seeds needed to generate a sapling will vary positively with sapling mortality rates.

Mature tree height

The last factor to be included, fecundity, represented by reproductive effort (seed number × seed mass), is especially relevant in the context of seed limitation. However, using reproductive effort as a variable results in circularities, because seedfall is incorporated in the response variable and seed mass is treated as a separate factor, so again we must turn to a proxy variable. Species attaining canopy stature are taller and broader crowned than understory treelets (Terborgh & Petren 1991), and thus benefit from greater energy budgets and commensurately greater seed production (Rüger et al. 2012). We shall therefore use the height of large mature individuals of each species as a proxy for reproductive effort in the expectation that species attaining greater heights will produce more seeds than species of lesser stature.

Dispersal mode

Some authors have noted differences in seeds per recruit and/or recruitment distance in relation to dispersal mode (e.g., Hubbell 1979). This being the case, dispersal mode could be expected to explain some portion of the variance.

ANALYSES

We log transformed all continuous variables (seeds per recruit, seed mass, mortality, tree height) to achieve normality. We first performed an exploratory data analysis by calculating pairwise correlations between all continuous variables and the categorical variable, dispersal mode. We then performed a linear regression analysis treating log seeds per recruit as the response variable, and the logs of seed mass, mortality, and tree height as the covariates. To investigate whether or not dispersal mode had an effect, we performed an ANOVA to compare the previous model (without dispersal mode) and the extended model (with dispersal mode). Residual diagnostics were conducted to check assumptions for linear models.

Based on the results of correlation, regression, and ANOVA, we performed structural equation modeling (SEM) following the workflow proposed by Grace (2006). We first constructed a path diagram including both direct and indirect effects from covariates to response as the initial model (full model) as suggested by the exploratory analysis. We treated dispersal mode as a composite variable by setting a dummy variable for each category (Grace et al. 2010). We then estimated the path coefficients for the initial model (full model), and set the non-significant path coefficients to zero to reach the final model. We re-checked the residuals for the final model, and reported standardized path coefficients so that all significant effects are comparable.

Finally, we conducted two additional univariate regressions to answer questions suggested by the results of the SEM analysis. First, we compared the results obtained with the more complex model to a simple linear regression of the log dry weight of seeds (i.e., reproductive effort) per small sapling recruit vs. log tree height for both gross seedfall and intact seeds. Second, we regressed the log dry mass of seeds per small sapling recruit vs. log density of seed-bearing mature trees in the population as a test of negative density dependence.

All statistical analyses were performed in R version 2.15.0 (R Development Core Team 2012).

RESULTS

General considerations

Gross seedfall for all woody species in the community was 376,014 in 46,894 records (presence of one or more seeds of a given species in a trap on a given collection date). Of the total, 124,991 (33%) represented intact seeds. Approximately 500 taxa (trees, treelets, lianas, and epiphytes) contributed to these totals. Unknowns constituted an insignificant fraction, 0.0018. The number of seeds per species was highly skewed, as only seven small-seeded species (not included in the analysis; five of them *Ficus* spp.), contributed 50% of gross seedfall.

Based on gross seed production, reproductive effort varied from 13,040 g (dry weight) of seeds/ha-yr for *Clarisia racemosa* to 9.3 g/ha-yr for *Justicia appendiculata* (Table A1). The corresponding values for intact seeds were 6,920 g/ha-yr for *Clarisia racemosa* and 9.3 g/ha-yr for *Justicia appendiculata*.

The overall rate of sapling recruitment (all species) proved quite variable, ranging from a high of 531 per ha-yr in 1998-2002 to a low of 165 per ha-yr in 2006-2010. The surge of recruitment registered in the 2002 census reflected the prior occurrence of several major treefalls in the plot, whereas the ensuing eight years were a period of relatively low treefall activity. For the purpose of the analyses to follow, we use the mean recruitment rate for each species, as documented over the 12-yr period from 1998 to 2010.

Species specific recruitment rates for small saplings varied over more than an order of magnitude, from 18.0 per ha-yr for *Rinorea viridifolia*, the most abundant understory treelet, to 0.85 per ha-yr for three uncommon species. The recruitment rate per species was related to the density of reproductive female trees in the population ($N = 89$, $R^2 = 0.29$, $F = 34.9$, $p < 0.001$). However, the recruitment rate of small saplings was not associated with any of the following: the number of intact seeds falling per ha-yr ($N = 75$, $R^2 = 0.001$, $F = 0.050$, $p > 0.1$), seed mass ($N = 75$, $R^2 = 0.008$, $F = 0.552$, $p > 0.1$, both by linear regression), or dispersal mode ($N = 75$, $R^2 = 0.079$, $F = 0.885$, $p > 0.1$, by ANOVA).

Number of seeds per recruit varied over >3 orders of magnitude from a minimum of 9.5 in the case of *Klarobelia candida*, a strongly shade tolerant treelet, to 46,191 for *Sapium marmieri*, a small-seeded, light-demanding gap colonizer that attains canopy stature.

Statistical analyses

The exploratory data analyses and linear model analyses suggested that taller trees produced many more seeds per sapling recruited (Figure 1). The log transformed continuous variables (seeds per recruit, seed mass, mortality, and tree height) were normally distributed (histograms in Figure 1). Among them, the only significant pairwise correlations were (1) a positive correlation between tree height and seeds per recruit ($r = 0.437$, $p < 0.01$); and (2) a positive correlation between tree height and seed mass ($r = 0.408$, $p < 0.01$). Dispersal mode had little or no explanatory power in the pairwise correlations (color-coded points in Figure 1).

Multivariate linear regression confirmed the relationships in Figure 1: tree height had significant positive effect ($\beta = 1.238 \pm 0.279$, $t = 4.431$, $p < 0.001$), seed mass had significant negative effect ($\beta = -0.463 \pm 0.158$, $t = -2.927$, $p < 0.01$), and mortality had insignificant negative effect ($\beta = -0.308 \pm 0.351$, $t = -0.877$, $p > 0.1$) on seeds per recruit.

Overall, the regression model explained 32% of the variance in seeds per recruit (R^2 = 0.323, $F = 6.99$, $p < 0.001$). Residual diagnostics suggested all linear assumptions were satisfied. Comparing the previous model with an extended model that included dispersal mode revealed that dispersal mode could not significantly increase the variance explained (ANOVA, $F = 0.273$, $p > 0.1$). Thus, the results of the multivariate linear regression were robust. The overall results were insensitive to whether we used gross seedfall or intact seeds to represent seeds per recruit.

Structural equation modeling (SEM) indicated that tree height had a strong positive effect on seeds per recruit, partially mediated by a negative indirect effect through seed mass (Figure 2). Because tree height emerged as having the strongest effect on seeds per recruit, we constructed the SEM by including both a direct path from tree height, and indirect paths through dispersal mode, seed mass, and mortality to seeds per recruit (Figure 2). Several path coefficients in the initial model were found to be insignificant (dashed lines in Figure 2), leading to the reduced final model (solid lines in Figure 2). With only two covariates, tree height and seed mass, the final model explained a substantial proportion of the observed variance in seeds per recruit ($R^2 = 0.311$). Residuals for the final model were re-checked to ensure SEM assumptions were satisfied. The strongest relationship was the positive direct effect from tree height to seeds per recruit ($\gamma = 0.592$), followed by the positive indirect effect from tree height to seed mass ($\gamma = 0.408$) and the negative indirect effect from seed mass to seeds per recruit ($\gamma = –0.379$). Because standardized path coefficients are directly comparable among effects (Grace and Bollen 2005), the final model suggested that the overall positive effect from tree height to seeds per recruit was dominated by the strong positive direct effect, partially mediated by the negative indirect effect through seed mass (0.437 = 0.592 + (0.408 × (–0.379))). Thus, the direct positive effect from tree height to seeds per recruit (0.592) was stronger than the apparent correlation (0.437). These results were substantially confirmed by a simple linear regression using log seed dry mass per recruit vs. log tree height in which tree height explained a larger proportion of the total variance, regardless of whether the response variable was based on gross seedfall ($R^2 = 0.43$, $F = 35.9$, $p < 0.001$) or intact seeds ($R^2 = 0.41$, $F = 32.5$, $p < 0.001$).

Finally, we asked whether the data provide evidence of negative density dependence in the seed-to-sapling transition by regressing the log seed mass per sapling recruit vs. log density of seed-bearing individuals in the population. Under negative density dependence, less common species might be expected to produce saplings at a lower reproductive cost (grams of seed) than more common species, predicting a positive relationship between reproductive effort and population abundance. To the contrary, no clear relationship emerged ($R^2 = 0.07$, $F = 3.3$, $p > 0.01$) and a slight negative trend ($\beta = –0.42$) was contrary to the prediction.

DISCUSSION

Given the strength of the positive relationship between tree height and seeds per recruit, a 40-m tall canopy tree must produce a seed mass 13 times greater than that of a 5-m tall treelet to make a sapling[*]. Using a somewhat different approach, King et al. (2006) came to a similar conclusion for the tree community at Barro Colorado Island, Panama. Why do understory treelets enjoy dramatically higher reproductive efficiency? Above, we reasoned that seed fates are determined by both intrinsic and extrinsic factors that determine survival to the sapling stage. Intrinsic factors (tree height, seed mass, and dispersal mode) plus a surrogate for an abiotic extrinsic factor (sapling mortality, a stand-in for microsite quality) accounted for approximately 30% of the variance in the SEM analysis. However, in the SEM analysis, a positive effect of seed mass on recruitment is offset by the fact that taller trees produce heavier (and hence relatively fewer) seeds than understory treelets. Thus a univariate analysis that employed seed mass directly in the response variable accounted for a larger proportion (41%) of variance.

Since large trees produce vastly more seeds than understory treelets, one could expect their seeds and seedlings to experience greater levels of crowding-induced mortality or negative density-dependence (Harms et al. 2000, Comita et al. 2010). We examined this possibility by regressing seed mass (i. e., reproductive effort) per recruit against the density of individuals expressing female function in the population and failed to expose a relationship. Two observations argue that crowding should be weak in our context. First, as stressed above, to a first approximation, only dispersed seeds produce saplings in this community (Terborgh and Nuñez-Ituri 2006; Terborgh et al. 2011). By

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[*] $\left(\frac{40\text{ m}}{5\text{ m}}\right)^{1.238} \approx 13$

using "intact" (mainly post-dispersal) seeds in the analysis, we attempted to avoid the additional variance that including undispersed seeds would have imposed on the response variable. Second, the rain of seeds dispersed away from parent trees, even of the most common tree species, is extremely scant, being $<1/\text{m}^2$-yr for all of the 48 species that entered the analysis. Experimental results indicate that effects of seedling competition become strong above 100 seedlings/m^2 (Weiner 1995), yet at Cocha Cashu tree seedlings occur at a mean density of only $5/\text{m}^2$ (Harms et al. 2004). We thus feel that seedling competition is unlikely to account for the large difference in the number of seeds needed to generate a sapling of a canopy tree vs. an understory treelet.

In the seed-limited environment of this forest, the proportion of seeds dispersed should have a direct effect on sapling establishment. Yet, virtually identical results were obtained whether we used gross seedfall (including undispersed seeds in ripe fruits, etc.) or intact seeds to construct the response variable. Although the result seems counterintuitive, it is explained by a strong interspecific correlation between the gross seedfall and the rain of intact seeds ($r = 0.96$).

There is a potential interaction between dispersal and tree height in the fact that there is a clear stratification of dispersers in relation to body mass. Large bodied dispersers such as Ateline primates and Cracids need large branches for support and typically feed in the canopy. The understory zone below 10 m is occupied by treelets unable to support large-bodied dispersers. Consequently, treelets are mostly dispersed by small mammals such as squirrel monkeys, tamarins and marsupials, along with small birds and bats. Despite these differences, dispersal mode explained essentially none of the variance in number of seeds per sapling.

The influence of seed mass (per seed) on seeds per sapling was negative, as expected, but weak relative to the effect of tree height. A stronger relationship might have resulted had there been a rigid interspecific tradeoff between seed mass and seed number. However, interspecific differences in seed mass appear to have been largely swamped by the much stronger relationship between seed number and mature tree height. The influence of seed mass could also have been weakened somewhat by the fact that the smallest seeds were certainly undercounted as they tend to disappear into the debris that collects in the traps. Another minor source of error was that the seeds of some uncommon treelets were so rare that they may sometimes have been put aside as unknowns. These biases could have affected the values used for a small number of species out of the 48 analyzed, but any resulting distortions were clearly minor in relation to the robust outcome of the analysis.

Finally, we come to the central question of how the seeds of treelets can be possessed of so much more survival potential than those of canopy trees. One could devise hypotheses based on intrinsic differences (e.g., seeds/seedlings of treelets are more likely to establish in shade or are better defended from enemies), but we know of no support for such claims. There is, however, a consistent intrinsic difference between canopy trees and understory treelets that does not involve properties of their seeds or seedlings: it is their fecundity. Many fully reproductive treelets produce only a few dozen seeds a year. Such a meager production is unlikely to attract seed/seedling predators and even more unlikely to favor the evolution of host-specialized seed or seedling predators or pathogens (Álvarez-Loayza and Terbogh 2011). If this argument is valid, the propagules of treelets are better able to hide from their enemies in space than their taller, more fecund, counterparts. This reasoning is consistent with the Janzen (1970)-Connell (1971) hypothesis of escape in space from host-specific enemies (Carson et al. 2008, Terborgh 2012). While only suggested by the results presented, we view an interpretation based on Janzen-Connell as inherently plausible, consistent with the facts and amenable to test in future research.

ACKNOWLEDGMENTS

We thank INRENA/SERNANP (Peruvian park service) administrators in Cusco and Lima for the many permits that allowed this research to unfold for more than 20 years. We are deeply grateful to legions of assistants, far too numerous to name, who contributed to the fieldwork. We thank Jim Grace and Dean Urban for statistical advice. The Andrew Mellon Foundation and National Science Foundation (DEB 0742830) are gratefully acknowledged for financial support. We also thank several anonymous reviewers for myriad suggestions.

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SUPPLEMENTARY MATERIAL

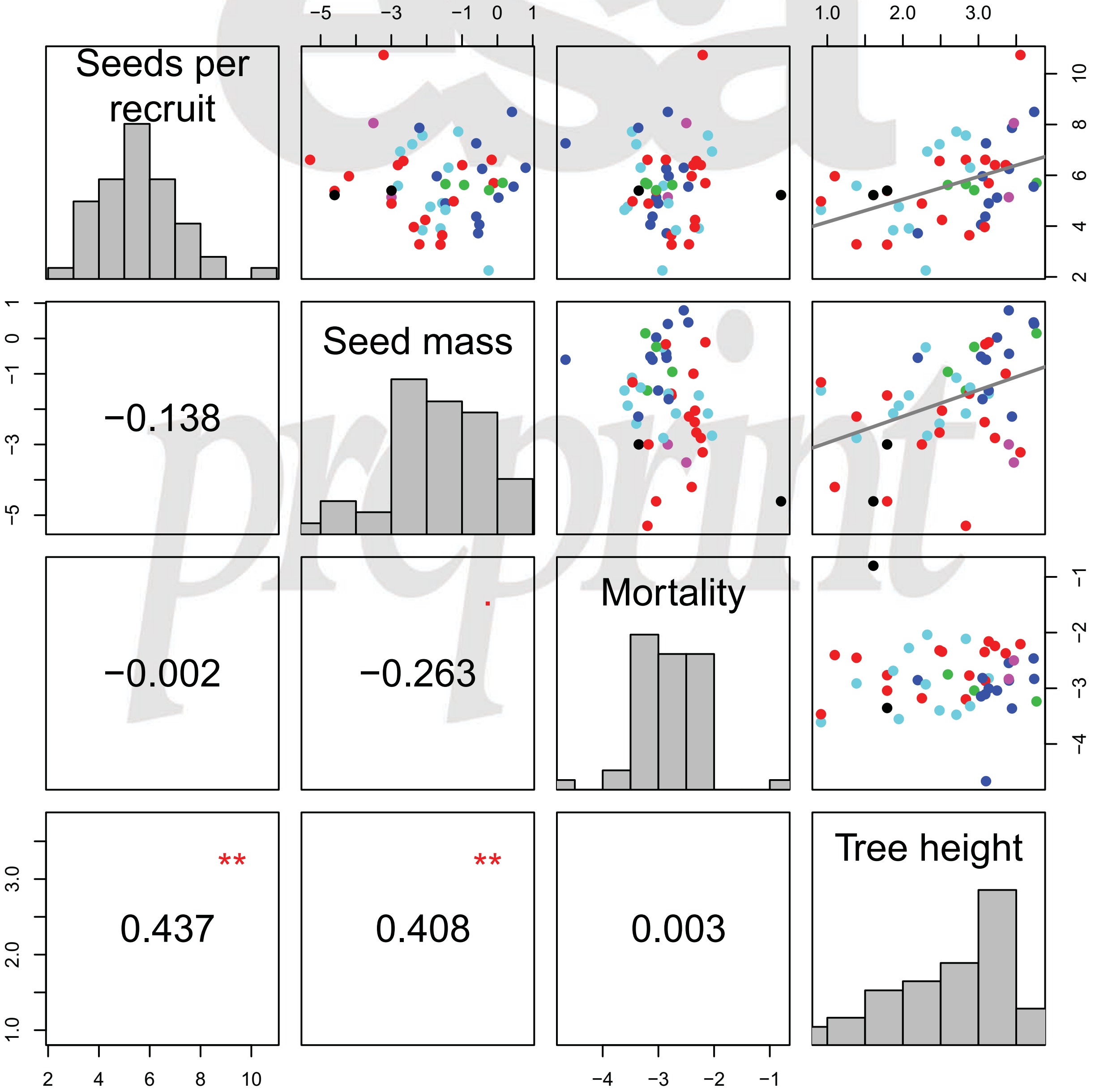
Appendix A

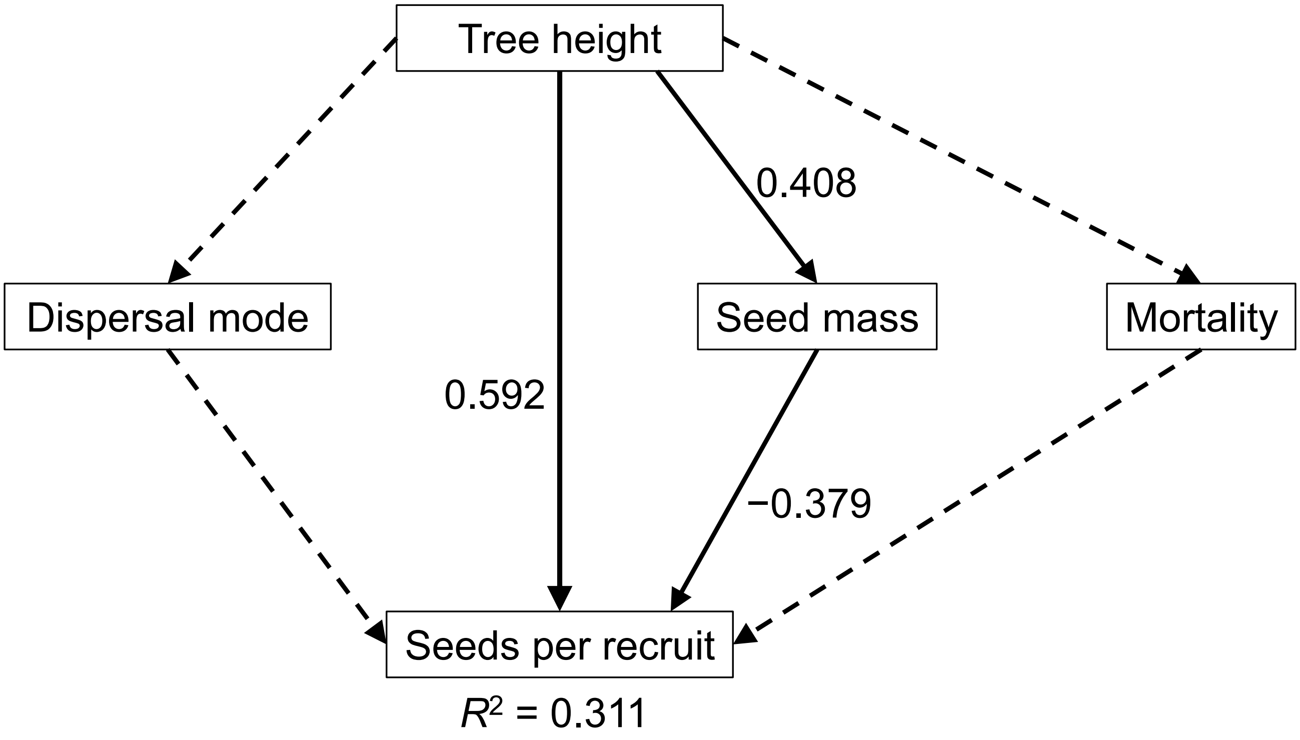
Table A1. Data used in calculating the reported results for 48 species of trees and treelets at Cocha Cashu Biological Station in Perú.

FIGURE LEGENDS

Figure 1. Relationships between intact seeds per recruit, seed mass, small sapling mortality (a surrogate for microsite quality), and tree height (a surrogate for fecundity) for 48 species of trees and treelets. Log-transformed values are shown as histograms in the diagonal panels. Upper panels are pairwise scatterplots between these four variables, color coded by dispersal mode (black: autochorous, red: bird, green: bat, blue: large primate, cyan: small arboreal mammal, magenta: unknown, and yellow: wind). Lower panels are correlation coefficients with significance tests (**: $p < 0.01$), suggesting two significant correlations, represented by regression lines in the upper panels (tree height vs. seeds per recruit, tree height vs. seed mass).

Figure 2. Results of structural equation modeling (SEM) for the direct effect from tree height (to represent fecundity) and indirect effects through dispersal mode, seed mass, and sapling mortality (to represent quality of microsites) to seeds per recruit. The initial model includes all paths (dashed and solid lines), whereas the final model includes only significant paths (solid lines). Standardized coefficients, directly comparable for different effects, are shown for significant paths (solid lines, $p < 0.001$), and set to zero (not shown) for insignificant paths (dashed lines). Under the final model, the SEM explains 31% of the variance.


Seeds per recruit
Seed mass
Mortality
Tree height
−0.138
−0.002
−0.263
0.437
**
0.408
**
0.003
−5
−3
−1
0
1
1.0
2.0
3.0
10
8
6
4
2
1
0
−1
−3
−5
−1
−2
−3
−4
3.0
2.0
1.0
2
4
6
8
10
−4
−3
−2
−1


Tree height
Dispersal mode
Seed mass
Mortality
Seeds per recruit
0.408
0.592
−0.379
R^2 = 0.311