100 YEARS Journal of Ecology British Ecological Society

Journal of Ecology doi: 10.1111/1365-2745.12027

Life-history trade-offs during the seed-to-seedling transition in a subtropical wet forest community

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Summary

1. The transition from seed to established seedling (STS) represents a major bottleneck in plant demography with implications for community dynamics and the maintenance of species diversity. The relative strength of seed limitation versus seedling establishment limitation can reveal life-history trade-offs that contribute to the maintenance of community diversity. If seed limitation dominates, chance arrival to open sites may play a key role in maintaining diversity. If seedling establishment limitation dominates, however, species relative abundances may depend more on tolerance to environmental and biotic conditions during seedling establishment (i.e. species-specific regeneration niche).

2. We used three years of seed rain and seedling recruitment data for 19 species of tropical woody plants collected in the Luquillo Forest Dynamics Plot in Puerto Rico to (i) examine a trade-off between seed and seedling establishment limitation and (ii) quantify the biotic and abiotic factors that mediate the STS transition.

3. We did not find evidence of a life-history trade-off in the form of a negative correlation between seed and seedling establishment limitation. However, species varied considerably in the relative levels of seed and seedling establishment limitation they displayed. Seed mass correlated negatively with seedling establishment limitation but not with seed limitation. We found striking differences in STS transition between life-forms categorized as trees (including two palms) and lianas; lianas exhibited significantly higher STS transition rates than trees.

4. The biotic and abiotic variables most strongly associated with successful STS transition differed between life-forms. For trees, conspecific seed density and temporal fruiting concentration had negative effects on seedling establishment, while seed mass had a positive effect. A significant interaction between leaf litter input at a plot and seed size suggested that large-seeded species had higher STS transition probability in plots with more leaf litter biomass. This effect was reversed for small-seeded species. For lianas, leaf litter had a negative effect on STS transition and temporal fruiting concentration had a positive effect.

5. *Synthesis*. Our analyses demonstrate the multidimensional axes of regeneration niches and how they can be related to seed size. Long-term data sets are critical for understanding these relationships because the relevant factors vary along large spatial and temporal scales.

Key-words: life-history trade-offs, Luquillo, plant population and community dynamics, Puerto Rico, regeneration niche, seed and seedling establishment limitation, successional niche

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Introduction

The life cycle of plants is comprised of several remarkable transitions, during which individuals are culled from populations through a variety of mechanisms (Grubb 1977; Harper 1977; Schupp 1995). The seed to established seedling (STS) transition is one critical bottleneck in plant demography (Poorter 2007) with implications for community dynamics (Levine & Murrell 2003) and species relative abundances. Life-history trade-offs (i.e. negative correlations between pairs of traits) that appear during the STS transition may be critical for creating and maintaining species diversity (Hubbell & Foster 1986; Pacala *et al.* 1996; Hubbell 2001).

A number of trade-offs may manifest during the STS transition. First, a negative relationship between competitive and colonization abilities (Levins & Culver 1971; Tilman 1994) can theoretically maintain diversity so long as a competitive dominance hierarchy is strictly maintained. This trade-off may appear during the STS transition as a result of differences in seed size among species, as small-seeded species are better colonizers (through higher fecundity or dispersal) and large-seeded species are better competitors (Everham, Myster & VanDeGenachte 1996; Coomes & Grubb 2003). However, empirical support for strict dominance hierarchies is limited (Coomes & Grubb 2003). A second plausible trade-off may occur between fecundity and stress tolerance (Muller-Landau 2010); more fecund species persist by establishing in sites with favourable conditions simply by arriving first (colonization advantage). Less fecund but more stress tolerant species are able to establish in unfavourable conditions (e.g. drought or shade) despite being more seed limited throughout the landscape. Finally, species may inhabit specific successional niches (Pacala & Rees 1998), which involve trade-offs in the ability of species to survive at low-resource conditions (e.g. shade) vs. the ability to exploit the temporary resource-rich conditions generated in the wake of disturbance (e.g. fast growth in high-light conditions). In the case of the STS transition, seedlings of early successional species may persist despite seed limitation because they are capable of high-seedling establishment in recently disturbed sites (e.g. high-light environments) (Dalling, Winter & Hubbell 2004). Nevertheless, it is important to note that the trade-off in this model may be manifest at different life-history stages (e.g. sapling or adult tree demography). Together, these three mechanisms illustrate how trade-offs between life-history traits may interact with environmental heterogeneity to drive successional dynamics and maintain diversity (Chesson 2000).

Conditions that mediate life-history trade-offs during the STS transition can be generally partitioned into those that limit dispersal (i.e. seed limitation) and those that limit seedling establishment (i.e. safe-site limitation) (Turnbull, Crawley & Rees 2000; Muller-Landau *et al.* 2002; Norden *et al.* 2009; Uriarte *et al.* 2010). Because seed arrival at a site precedes seedling establishment, the role of environmental heterogeneity in governing species distributions may depend on the relative strength of seed vs. seedling establishment limitation. Seed limitation can result from either limited production (low fecundity) or restricted dispersal of available seeds (Clark, Macklin & Wood 1998; Terborgh *et al.* 2011). Following dispersal, seedling establishment can be limited by the post-dispersal action of a wide variety of biotic and abiotic mechanisms (Muller-Landau *et al.* 2002; Norden *et al.* 2007a, b). Examining the relationship between seed and establishment limitation, and how each relates to seed size, can shed light on the processes governing the STS transition.

The particular mechanisms that regulate the STS transition involve a variety of biotic factors such as seed predation, herbivory and competition, all of which can be exacerbated by high seed and seedling densities (Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Comita *et al.* 2009). In addition, abiotic factors, such as light availability and leaf litter conditions interact with seed and seedling physiology and life-history traits to influence the likelihood that seeds germinate and become established seedlings in heterogeneous environments (e.g. Pearson *et al.* 2002; Masaki *et al.* 2006; Norden *et al.* 2009).

Examining how trade-offs associated with dispersal and stress tolerance vary between life-forms and successional stages may help determine how the processes that govern the STS transition differ among groups of ecologically similar species. Lianas (woody vines) and trees represent different life-history strategies in tropical forests (Schnitzer & Bongers 2002). While previous studies comparing these groups have focused on the physiology of mature plants (Schnitzer 2005; Cai, Schnitzer & Bongers 2009; Walt *et al.* 2010), a limited body of work suggests a similar growth/survival trade-off between life-forms during early life stages (Gilbert *et al.* 2006; Cai *et al.* 2007). Despite the increasing attention given to liana dynamics in tropical forests (Schnitzer 2005; Schnitzer & Bongers 2011), we lack a detailed understanding of the dynamics of early life-history stages that are critical in the maintenance of liana diversity. Another contrast exists between species associated with different successional stages. Pioneer species are typically associated with high fecundity, widespread dispersal and relative intolerance to environmental stress and limited resources. In contrast, late successional species tend to be less fecund and more robust to environmental stress and limited resources. As a result, species associated with different successional stages may display different responses to environmental heterogeneity.

Here, we employ seed rain and seedling establishment data collected over three years at the Luquillo Forest Dynamics Plot in Puerto Rico to explore how environmental heterogeneity and variation in life-history characteristics (e.g. seed size, life-form, successional association) influence the STS transition for 14 tree species (including 2 palms) and 5 liana species. We framed our study with two primary questions:

1. Are there trade-offs in the strength of seed vs. seedling establishment limitation that are mediated by seed size? We predicted a trade-off between seed arrival and seedling establishment limitation, with larger-seeded species being more seed limited (i.e. relatively low fecundity and dispersal, and greater predation) and smaller-seeded species

more limited by seedling establishment (i.e. relatively narrow regeneration niches and low competitive ability and stress tolerance).

2 What are the biotic (i.e. seed size, life-form and con- and heterospecific seed density) and abiotic (i.e. light and leaf litter) factors that mediate the STS transition? If differences in seed size reflect a life-history trade-off relevant to the STS transition, we expected to find significant interactions between seed size and abiotic conditions. Specifically, we expected STS of small-seeded species to be influenced positively by light (competitive ability) and negatively by leaf litter (stress tolerance) relative to large-seeded species. We expected this prediction to vary across successional groups (i.e. small-seeded pioneers versus relatively large-seeded shade-tolerant species) and that trees and lianas would show similar patterns.

Materials and methods

STUDY SITE

The Luquillo Forest Dynamics Plot (LFDP) is a 16-ha permanent plot (18°20′°N, 65°49′°W) in north-eastern Puerto Rico. Classified as subtropical wet forest in the Holdridge life-zone system (Ewel & Whitmore 1973), mean annual rainfall in the LFDP is 3,500 mm year^{-1} and elevation ranges from 333 to 428 m a.s.l (Thompson *et al.* 2002). Soils are formed from volcaniclastic rock (Soil Survey Staff 1995). The LFDP has experienced a series of severe natural and human disturbances (Scatena & Larsen 1991; Thompson *et al.* 2002; Beard *et al.* 2005). Tropical storms have produced a highly dynamic community and some of the key processes that influence community composition have been identified (e.g. Uriarte *et al.* 2005, 2009). In addition, portions of the LFDP were used for agriculture and logging before 1934 (Thompson *et al.* 2002). As a result, the plot contains a mix of species representative of different successional stages and can be roughly divided into 'high' and 'low' sections of historic land-use intensity (Fig. S1 in Supporting Information; Uriarte *et al.* 2009).

SEED RAIN AND SEEDLING PLOTS

Every two weeks, all fruits and seeds were collected from a network of 120 phenology baskets (Fig. S1; Zimmerman *et al.* 2007). These 0.5-m^2 baskets are constructed with 1-mm mesh mounted 1 m above the ground. Three 1-m^2 seedling plots are located 2 m away from each phenology basket (plot $n = 360$). We refer to each phenology basket and its three associated seedling plots as a 'station'. Each year, all seedlings (all germinated woody stems < 1 cm diameter at 1.3 m (DBH)) are counted, tagged and identified to species. Censuses took place between 22 March and 20 April in 2007, 3 March and 11 April in 2008, 9 March and 18 June in 2009 and 5 March and 9 April in 2010.

We applied the seed rain data from each phenology basket to each of the three associated seedling plots. As a result, the number of observed seedlings in a seedling plot sometimes exceeded the number of seeds counted in the corresponding phenology basket. Previous analyses (Hille Ris Lambers, Clark & Beckage 2002; Wright *et al.* 2005) addressed this issue by setting the number of seeds equal to seedling recruits for these observations. We followed this convention when calculating seed and seedling establishment limitation (see Seed and seedling establishment limitation below). This approach, however, results in a mean per-seed STS transition probability (i.e. number of seedling recruits/number of seeds) equal to one, artificially indicating 'ideal' conditions for establishment. Because this is both biologically unrealistic and mathematically problematic for the models of the STS transition we used, we introduced a conservative bias in our results by excluding these observations from our model of STS transition described below (see Appendix S1 for details about excluded observations).

SPECIES SELECTION

To ensure sufficient statistical power, we selected focal species based on two criteria over the three years combined: (i) seeds (and seedlings) were recorded from $\geq$ 10 baskets (and plots) and (ii) seed (and seedling) densities must have varied by at least a factor of four among baskets (and plots). These criteria resulted in 19 focal species that represent a broad range of seed sizes, successional status, dispersal modes and evolutionary histories (Table 1). Fourteen of these species account for *c.* 79% of tree stems $\geq$ 10 cm DBH recorded live in the LFDP during the 2005 census. Although lianas are not included in LFDP tree censuses, they are included in the seedling censuses. In total, the 19 focal species account for > 95% of all seedlings recorded in each census from 2008 to 2010.

SEED AND SEEDLING ESTABLISHMENT LIMITATION

To determine whether seed size influenced the relative strength of seed and seedling establishment limitation for each species (Question 1), we quantified the proportion of baskets not reached by seeds ('fundamental seed limitation' sensu Muller-Landau *et al.* 2002) as:

$$Seedlimitation_i = 1 - \frac{a_i}{n} \qquad \text{eqn 1}$$

where a is the number of stations with seeds of species i, divided by the total number of stations, n (here, $n = 120$). The difference between seed limitation and new seedling establishment provides an index of safe-site limitation ('realized establishment limitation' sensu Muller-Landau *et al.* 2002), calculated as:

$$Seedling\ establishment\ limitation = 1 - \frac{r_i}{6a_i} \qquad \text{eqn 2}$$

where r is the number of seedling plots with seedling recruits of species i. We multiplied a_i by 6 because seeds from each basket (0.5 m^2) were used as an estimate of seed rain for each of the three adjacent (1-m^2) seedling plots. These calculations were based on the full data set of total seed rain and seedling establishment across all three study years. We used a

Table 1. Characteristics of focal species

Code	Species	Family	Life-form	Successional group*	Seed mass† (g)	Total observed seeds	Total observed recruits	Mean per-seed success‡	Primary dispersal vector§
AF	*Alchorneopsis floribunda* (Benth.) Muell. Arg.	Euphorbiaceae	Tree	Pioneer	0.007	16,455	11	0.003	A
CS	*Cecropia schreberiana* Miq.	Urticaceae	Tree	Pioneer	0.001	369,755	70	0.000	A
CD	*Chionanthus domingensis* Lam.	Oleaceae	Tree	Secondary	0.54	132	21	0.047	A
DE	*Dacryodes excelsa* Vahl	Burseraceae	Tree	Late	1.255	4,583	665	0.074	A
DG	*Drypetes glauca* Vahl	Putranjivaceae	Tree	Late	0.365	101	21	0.087	A
GG	*Guarea guidonia* (L.) Sleumer	Meliaceae	Tree	Secondary	0.251	682	398	0.219	A
HL	*Heteropteris laurifolia* (L.) A. Juss.	Malpighiaceae	Liana	–	0.072	1,007	707	0.215	W
HV	*Hippocratea volubilis* (L.)	Celastraceae	Liana	–	0.1	3,258	2,107	0.289	W
MB	*Manilkara bidentata* (A. DC.) A. Chev.	Sapotaceae	Tree	Late	0.594	278	39	0.044	A
MD	*Matayba domingensis* (DC.) Radlk.	Sapindaceae	Tree	Late	0.161	580	68	0.059	A
OL	*Ocotea leucoxylon* (Sw.) Laness	Lauraceae	Tree	Secondary	0.177	204	22	0.045	A
PP	*Paullinia pinnata* (L.)	Sapindaceae	Liana	–	0.395	205	109	0.186	A
PM	*Prestoea montana* (R. Graham) G. Nicholson	Arecaceae	Palm	Secondary	0.733	14,074	4,046	0.158	A
RS	*Rourea surinamensis* Miq.	Connaraceae	Liana	–	0.145	9,484	4,479	0.190	A
RB	*Roystonea borinquena* O. F. Cook	Arecaceae	Palm	Secondary	0.309	779	121	0.071	A
SM	*Schefflera morototoni* (Aubl.) Decne. & Planch.	Araliaceae	Tree	Pioneer	0.001	12,024	190	0.025	A
SV	*Securidaca virgata* (Sw.)	Polygalaceae	Liana	–	0.051	824	445	0.180	W
TH	*Tabebuia heterophylla* (DC.) Britton	Bignoniaceae	Tree	Secondary	0.011	5,062	281	0.027	W
TB	*Tetragastris balsamifera* (Sw.) Kuntze	Burseraceae	Tree	Late	1.14	444	47	0.064	A

*Successional group is based on information from Devoe (1989).

†Dry seed mass (g).

‡Mean per-seed success is calculated as the number of recruits divided by seeds (with the observed number of seeds from a trap applied to each of three associated seedling plots).

§Dispersal mode follows Devoe (1989) and Uriarte *et al.* (2005): A=animal, W=wind.

randomization procedure (see Appendix S2 for details) to determine whether observed levels of seed and seedling establishment limitation differed significantly from a null model in which seeds and seedlings were Poisson distributed across stations (Norden *et al.* 2009). The difference between the mean expected and observed seed limitation (δ_{Seed}) and seedling establishment limitation ($\delta_{\mathrm{Establishment}}$) ranges between -1 and 1; positive values indicate higher limitation than expected and vice versa. While these calculations assume a uniform distribution of potential seed sources across the sample area, many species in the LFDP are non-randomly associated with land-use history (Thompson *et al.* 2002; Uriarte *et al.* 2009). As a result, we calculated δ_{Seed} and $\delta_{\mathrm{Establishment}}$ separately for each of the two main land-use portions of the LFDP and assessed the difference between these categories for both δ_{Seed} and $\delta_{\mathrm{Establishment}}$.

To determine mean per-seed success for each species, we calculated the total number of established seedlings divided by six times the total number of seeds in the phenology baskets recorded during the study (to standardize sampling effort). This metric averages over environmental heterogeneity and provides a general picture of the STS transition. Next, we discuss the data and methods used to explore the influence of specific biotic and abiotic variables on STS transition in the LFDP.

ABIOTIC FACTORS

Light

To measure light availability at each plot around the time of the seedling censuses, we used hemispherical photography and an automated thresholding algorithm (Jonckheere *et al.* 2005) to calculate percentage light transmission. Photographs were taken soon after dawn in uniform light conditions without direct sunlight or rain on the lens using a Sigma 4.5 mm F2.8 EX DC fisheye lens mounted on a Nikon Coolpix camera (Nikon Corporation, Tokyo, Japan) and levelled at 1-m in the centre of each plot. Percentage light transmission calculated from photographs taken after each seedling census was used as a predictor variable for STS transition in the following year. Data are available upon request from the Luquillo LTER data repository (http://luq.lternet.edu/data).

Leaf litter

Leaf litter was collected in the phenology baskets every two weeks from August 2006 to August 2007, oven dried at 70 °C, and weighed. Here, we assumed that spatial variation among stations in leaf litter input remained constant over the three years of the study. This assumption is reasonable because (i) there were no large disturbances during this period and the climatic conditions remained relatively uniform, (ii) observations near the study site suggest that in the absence of severe disturbance, spatial variation in leaf litter exceeds temporal variation (D. Garcia-Montiel *unpublished data*) and (iii) our interest was in the impacts of relative spatial variation in leaf litter biomass, not absolute values. We calculated annual leaf litter input for each station (g m^{-2}) and applied this value to the associated plots for subsequent analyses.

BIOTIC FACTORS

Temporal concentration of seed production

Fruiting phenology of our focal species differs dramatically, with some species being most productive within short periods and others producing more consistently through the year (Fig. S2; Zimmerman *et al.* 2007). We predicted that species that produce seeds in concentrated bursts would have lower STS than those with less temporally variable seed production because they might suffer more from negative density-dependent factors (following section), and also that they might be exposed to sources of mortality for a longer time depending on the time between the fruiting peak and the subsequent seedling census. We might expect a high STS if a fruiting peak occurred shortly before a seedling census but given the phenology of our study species (Fig. S2) we expect this effect to be weak. We used the mean length of the fruiting vector calculated by Zimmerman *et al.* (2007) as a measure of temporal concentration of seed production.

Conspecific and heterospecific seed density

Negative density dependence factors (NDD) can influence the survival of tropical seedlings (Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Comita *et al.* 2009) and may be a critical process driving observed species abundance patterns in the LFDP (Comita *et al.* 2010). To tease apart the effects of NDD from conspecific vs. heterospecific seed density, we calculated the log (+1) transformed number of both conspecific and heterospecific seeds into each basket per year.

Seed size

We calculated species mean dry seed mass (g) by collecting and weighing 9–100 seeds per species (depending on abundance) from the Luquillo forest. Seed mass values were log-transformed prior to analyses because of the wide range of values among our study species (Table 1, Table S1 in Supporting Information).

Statistical Analyses

As values of δ_{Seed} and $\delta_{\text{Establishment}}$ were approximately normally distributed, we used linear regression to examine the relationship between δ_{Seed} and $\delta_{\text{Establishment}}$, as well as the relationship between each of these limitations and seed mass (Question 1). We expected that a competition/colonization or fecundity-stress trade-off would correspond to a negative correlation between δ_{Seed} and $\delta_{\text{Establishment}}$. If a trade-off occurs in the ability of species to survive in low-resource conditions (e.g. shade) vs. the ability to exploit the temporary resource-rich conditions generated in the wake of disturbance as predicted by the successional niche model, uncovering the pattern may hinge on the distribution of resources within the study area and time since disturbance. To test this, we used ANOVA and *t*-tests to compare δ_{Seed} and $\delta_{\text{Establishment}}$ among species of different successional groups (pioneer, secondary, late), life-forms (trees and lianas) and primary dispersal modes (animal vs. wind).

To evaluate specific factors associated with the STS transition (Question 2), we fit statistical models where the response variable was the number of seedlings recruited in individual seedling plots. The log of the number of seeds observed in each associated nearby seed basket was included as an offset. Initial model residuals exhibited over-dispersion so the results reported here are based on a generalized linear-mixed model with negative binomial errors. Abiotic covariates (light, leaf litter biomass), temporal fruiting concentration, the logarithm of seed mass, and conspecific and heterospecific seed density were included as fixed effects. Collinearity was less than 0.32 for all pairs of predictor variables. We also included a random effect for seedling plots nested within a single basket. To assess the evidence that the influence of abiotic factors on the STS transition was mediated by seed size, we examined interaction terms between abiotic factors and seed size in these models.

All continuous predictors were standardized prior to analyses by subtracting their mean and dividing by twice their standard deviation (Gelman & Hill 2006). This procedure enables a direct comparison of the magnitude and direction of covariate effects based on their estimated coefficients in regression analyses (Schielzeth 2010). Coefficients for all parameters were estimated using WinBugs (MRC Biostatistics Unit, Cambridge, UK) (Lunn *et al.* 2000) with weakly or non-informative priors, and models were judged to converge when R-hat for all parameters were less than or equal to 1.1 (Gelman & Rubin 1992). We determined statistical significance of predictor variables when 95% credible intervals did not overlap with zero. We calculated multilevel goodness-of-fit (R^2) using methods derived from Gelman and Pardoe (2006).

Results

QUESTION 1: ARE THERE SEED-SIZE MEDIATED TRADE-OFFS IN THE STRENGTH OF SEED VS. SEEDLING ESTABLISHMENT LIMITATION?

Although most species showed significant δ_{Seed} and $\delta_{\text{Establishment}}$ limitation, there was considerable variation in the degree of seed and seedling establishment limitation they displayed (Fig. 1, Table S2). In the low land-use portion of the plot δ_{Seed} and $\delta_{\text{Establishment}}$ were positively correlated ($P = 0.032$, Adjusted $R^2 = 0.20$) and not significantly correlated in the high land-use portion of the plot ($P = 0.27$). The positive correlation in the low land-use portion of the plot disappeared when one outlying species, *Tabebuia heterophylla*, was removed from the analysis. The relationship between $\delta_{\text{Establishment}}$ and log seed mass was negative and significant in both the low ($P = 0.002$, Adjusted $R^2 = 0.42$) and high ($P = 0.02$, Adjusted $R^2 = 0.22$) land-use portions of the plot (Fig. 2). The relationship between δ_{Seed} and seed mass, however, was not significant in either land-use portion of the plot (Fig. 2).

While species varied in the magnitude of δ_{Seed} and $\delta_{\text{Establishment}}$ between the two land-use portions of the plot, most species exhibited consistent patterns in the sign of each limitation regardless of land use. Across all species, the mean difference between land-use categories for δ_{Seed} was 0.18 (± SD 0.15), and for $\delta_{\text{Establishment}}$ was 0.13 (± SD 0.10), indicating that both limitations are stronger in the high land-use portion of the plot when averaged across species (Table 2). For most species, δ_{Seed} was significantly positive in both land-use portions of the plot while $\delta_{\text{Establishment}}$ showed more mixed results (Fig. 1 and Table S2).

We found some evidence for differences in $\delta_{\text{Establishment}}$ among successional groups (Table S3). In the low land-use portion of the plot, successional group had a significant effect on $\delta_{\text{Establishment}}$; pioneer species were more limited by seedling establishment compared with late successional species (Tukey's HDS, $P = 0.03$). Secondary forest species had intermediate levels of $\delta_{\text{Establishment}}$ that were not significantly different from either pioneer or late successional species. Successional group had no significant effect on δ_{Seed} values in either land-use portion of the plot (Table S3).

Life-form did not have a significant effect on either δ_{Seed} or $\delta_{\text{Establishment}}$; however, lianas had significantly higher levels of per-seed success than trees ($t = -5.7082$ two-tailed $P < 0.001$; Fig. 3). For all species pooled or for lianas alone, there was no significant relationship between seed mass and per-seed success but when considering trees alone there was a significant positive relationship (Fig. 3; $P = 0.046$, Adjusted $R^2 = 0.23$). This relationship became stronger when two outliers (*Prestoea montana* and *Guarea guidonia*) were removed ($P < 0.001$, Adjusted $R^2 = 0.68$). Primary dispersal mode (animal vs. wind) was not related to either δ_{Seed} or $\delta_{\text{Establishment}}$ (Table S3).

QUESTION 2: WHAT BIOTIC AND ABIOTIC FACTORS MEDIATE THE STS TRANSITION?

Several abiotic and biotic factors had significant effects on the probability of STS transition (Fig. 4). In the full model, life-form had the strongest effect on STS with lianas having significantly greater STS transition probability than trees. Goodness-of-fit for the data model was $R^2 = 0.20$. We subsequently ran separate models for each life-form to explore this variation. While light conditions did not have a significant

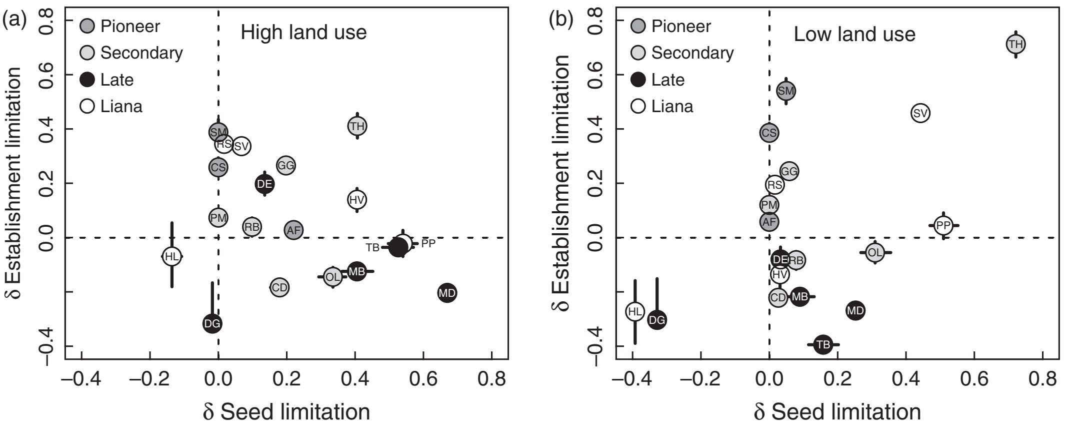

Fig. 1. Difference between observed and randomized seed and seedling establishment limitation (δ_{Seed} and $\delta_{\text{Establishment}}$) for 19 species in the low (a) and high (b) land-use intensity portions of the LFDP (see Table 1 for species codes). Positive values indicate higher limitation than expected by random and vice versa. Error bars represent 95% confidence intervals (see Table S2 for more details). Note that some error bars are too small to visualize.

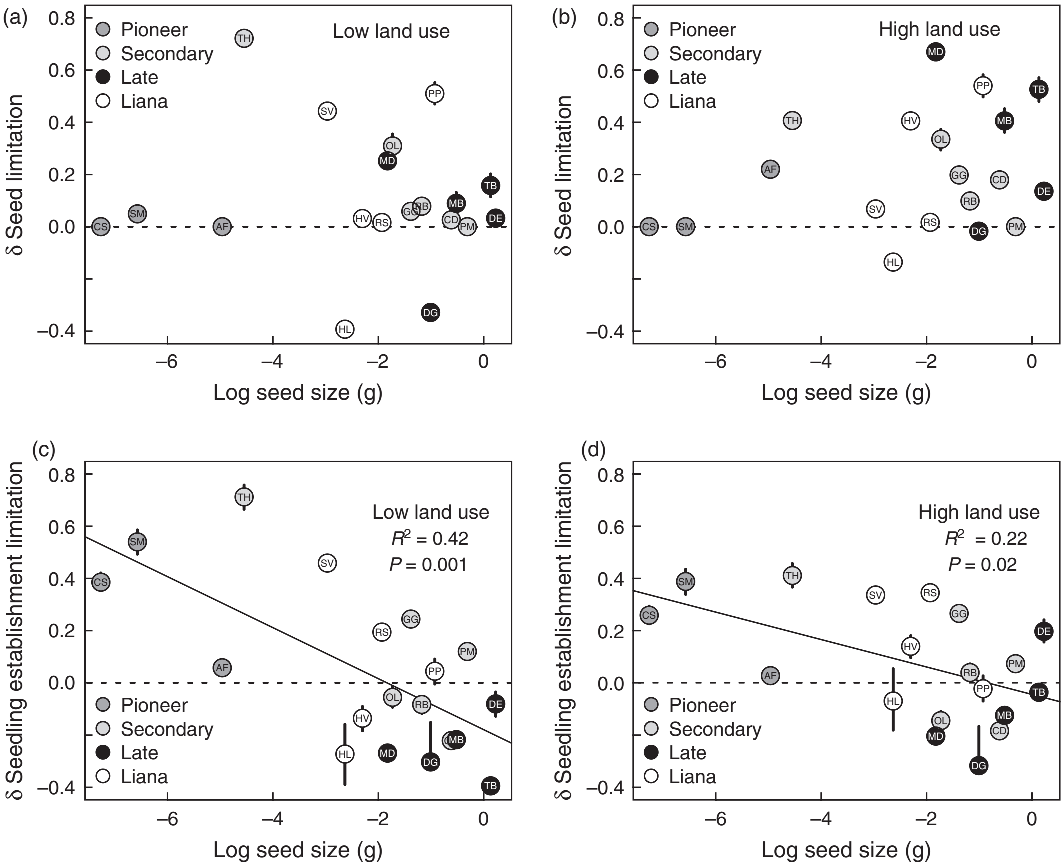

Fig. 2. Log-transformed seed mass (g) vs. δ_{Seed} (a, b) and $\delta_{\mathrm{Establishment}}$ (c, d) for the low (a, c) and high (b, d) land-use intensity portions of the LFDP. See Table 1 for species codes.

Table 2. The difference between observed seed and seedling establishment limitation in the low and high land-use intensity portions of the LFDP. Positive values indicate that the species was more strongly limited in the high land-use intensity relative to the low land-use intensity portions of the plot

Species	Land-use difference: Seed Limitation	Land-use difference: Seedling Establishment Limitation
AF	0.22	−0.03
CS	0.00	−0.14
CD	0.14	0.04
DE	0.10	0.26
DG	0.31	−0.02
GG	0.14	−0.02
HL	0.25	0.19
HV	0.37	0.27
MB	0.30	0.09
MD	0.42	0.06
OL	0.02	−0.10
PP	0.02	−0.08
PM	0.00	−0.05
RS	0.00	0.15
RB	0.02	0.11
SM	−0.05	−0.16
SV	−0.37	0.13
TH	−0.31	−0.31
TB	0.36	0.36

direct effect on the STS transition for either life-form, leaf litter biomass had a significantly negative effect for lianas. Mean fruiting vector was positively associated with the STS transition for lianas but negatively so for trees. Seed mass was positively associated with the STS transition for both life-forms but only significantly for trees. Heterospecific seed density did not have a significant effect on the STS transition for either life-form. Conspecific seed density had a significant negative effect on the STS transition for trees but not lianas.

We expected significant interactions between abiotic covariates and seed size to reveal a role of environmental factors in mediating the STS transition depending on seed size. We detected only one significant interaction between leaf litter biomass and seed size for trees but not lianas (Fig. 4). Small-seeded tree species had reduced STS in plots with higher levels of leaf litter biomass, while large-seeded species had slightly increased STS in plots with higher levels of leaf litter biomass.

Discussion

Considerable attention has been given to establishing the importance of life-history trade-offs in the maintenance of diversity in natural communities (Levins & Culver 1971; Pacala & Rees 1998). Trade-offs associated with seed size

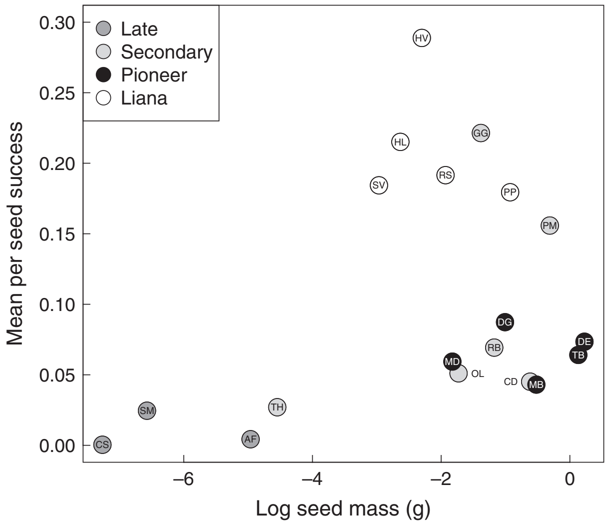

Fig. 3. Log-transformed seed mass and mean per-seed success for 19 focal species across all seedling plots and all three years (see Table 1 for species codes).

diversity has been of particular interest (Coomes & Grubb 2003; Moles & Westoby 2006; Muller-Landau 2010). Here, we paired hypotheses about life-history trade-offs with analyses of potential biotic and abiotic factors that might mediate them in natural systems. We discuss our results in the context of the maintenance of diversity in tropical forests.

QUESTION 1: ARE THERE TRADE-OFFS IN THE STRENGTH OF SEED VS. SEEDLING ESTABLISHMENT LIMITATION?

Nearly, all species examined here displayed strong seed limitation. By controlling for ‘source limitation’ (number of seeds), our null model tested for significant ‘dispersal’ limitation (sensu Muller-Landau *et al.* 2002). Therefore, if observed seed limitation differed by land-use history and δ_{Seed} did not, then we could conclude that observed seed limitation was due to source limitation (few or low fecundity adult trees) and not dispersal limitation. However, we did not find evidence for this relationship between land-use areas by successional group. Therefore, despite the observed relationships between

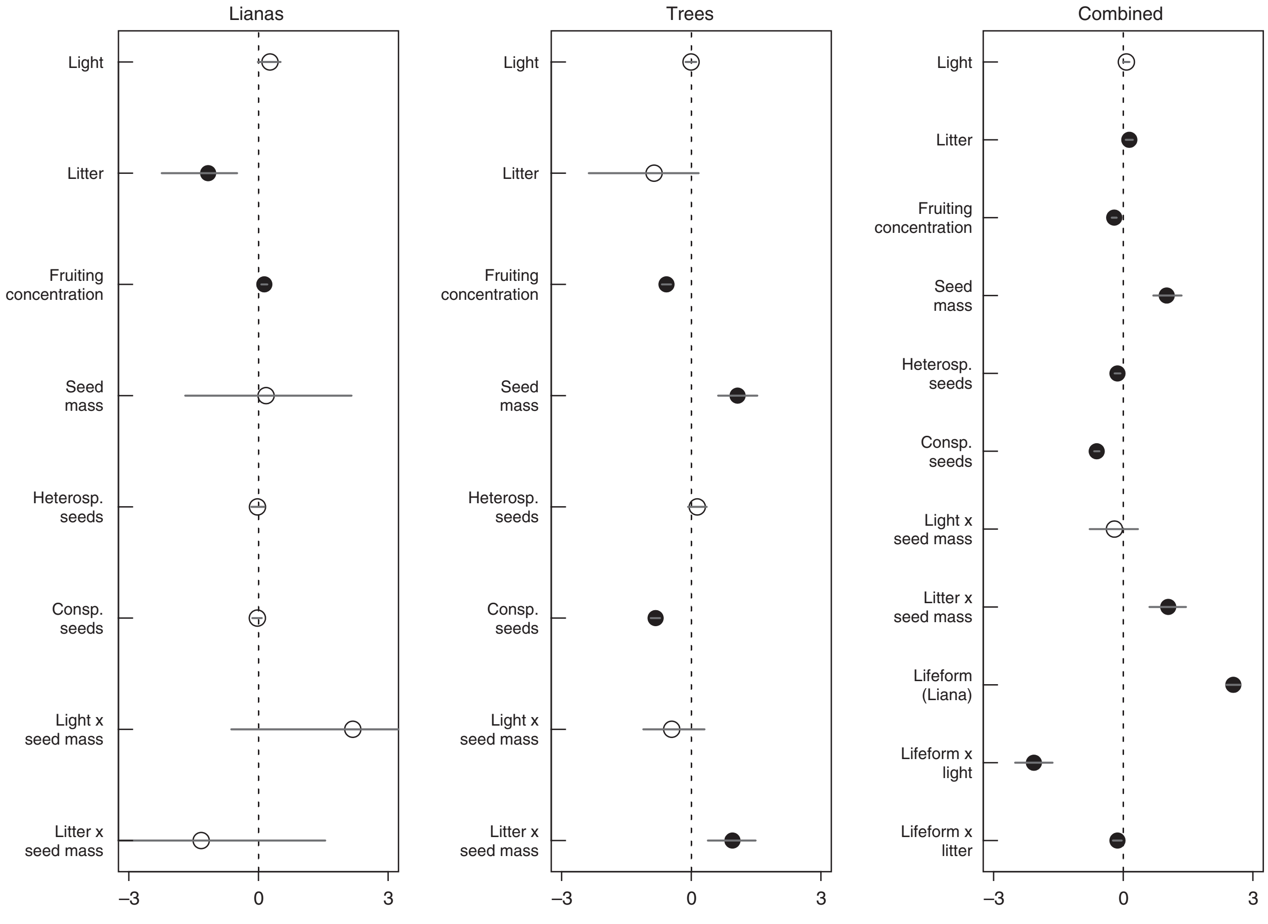

Fig. 4. Mean standardized coefficients and 2.5% and 97.5% credible intervals of the effects of abiotic and biotic covariates on STS transition probability in the LFDP. The response variable was the number of seedlings recruited in individual plots (see Methods: Statistical Analyses). These results are based on negative binomial generalized linear-mixed models with a log link. Filled circles indicate significant effects (i.e. credible intervals do not overlap zero).

mature tree abundances and land-use history in the LFDP (Thompson *et al.* 2002), our results are inconclusive about how seed limitation specifically contributes to differences in community composition across the LFDP.

We explicitly looked for a negative correlation between δ seed limitation and δ establishment limitation with the expectation that if a competition/colonization or fecundity-stress trade-off were operating, we would detect a negative correlation between these limitations. In fact, we found a positive correlation in the low intensity land-use portion of the plot. However, this unexpected relationship was largely dependent on one outlier species.

The relationship between δ_{Seed} and seed mass, predicted to be negative by the competition/colonization trade-off (Tilman 1994; Coomes & Grubb 2003), was not significant. One relatively large-seeded species (*P. montana*) accounted for 50% of stems $\geq$ 10 cm DBH in the 2005 tree census, and its dominance may have inflated measures of STS transition by overwhelming seed input. However, seed size was negatively related to $\delta_{\mathrm{Establishment}}$, as expected if trade-offs are mediated by seed-size-dependent stress tolerance (Muller-Landau 2010). The positive association between seed mass and per-seed success for trees also suggests a germination advantage for large-seeded species. These results conform with those of an experimental germination study of 119 Puerto Rican tree species (Francis & Rodriguez 1993), which found a positive relationship between seed mass and percentage of seeds germinating across a broad range of seed mass values (1.6×10^{-5} to 71 g). These results provide some support for a competition/colonization or fecundity-stress tolerance trade-off related to seed size (Tilman 1994; Coomes & Grubb 2003; Muller-Landau 2010), but demonstrate how large-seeded species (i.e. *P. montana*) can overcome seed limitation if they are very common as reproductive adults. A second species, *G. guidonia*, accounted for < 2% of stems $\geq$ 10 cm DBH in the 2005 tree census and its relatively high STS transition probability is more difficult to explain. One possibility is that *G. guidonia* experiences a recruitment bottleneck after the STS transition (Fernandez del Viso 1997).

We also found some evidence supporting the successional niche hypothesis. After controlling for variation in seed source abundance across land-use portions in the plot, pioneer species had higher seedling establishment limitation compared with late successional species in the low land-use intensity portion of the plot, indicating that successional groups may have differential seedling establishment success depending on land-use history (Comita *et al.* 2010).

QUESTION 2: WHAT BIOTIC AND ABIOTIC FACTORS MEDIATE THE STS TRANSITION?

Biotic drivers

Together with the observed negative relationship between seed mass and $\delta_{\mathrm{Establishment}}$, the positive effect of seed mass on STS transition for trees supports the notion that large seed size conveys tolerance to stress or competitive advantage. The most striking difference in STS transition probability in our analysis, however, was between lianas and trees. In this study, lianas had much higher STS transition probabilities than expected given their seed sizes. In addition, seedling establishment limitation was generally lower for lianas than trees despite spanning nearly the same range of seed limitation. Our results suggest a potential for differences among life-forms in terms of their regeneration niches.

One possible explanation for our findings is that lianas face more intense filtering in life stages beyond the STS transition. Unlike freestanding trees, lianas require auxiliary vertical support structures to facilitate their growth into the forest canopy (Schnitzer & Bongers 2002). It is feasible that this precarious lifestyle may impose higher selective pressure to succeed during the STS transition to increase the chance of establishing near a suitable support structure. Differences among species in terms of their seedling functional morphology (Garwood 1996; Ibarra-Manríquez, Martínez Ramos & Oyama 2001; Baraloto & Forget 2007) provide another possible explanation for our results. All species included in our study belong to two functional morphology types: cryptocotylar epigeal reserve (CER) and phanerocotylar epigeal foliar (PEF) *sensu* Garwood 1996;. All of the lianas belong to the CER-type, while all of the pioneer tree species belong to the PEF-type (C.J.N. pers. obs.). CER species tend to have relatively low relative growth rates and larger seeds than the PEF species (Ibarra-Manríquez, Martínez Ramos & Oyama 2001; Baraloto & Forget 2007).

We expected temporal concentration of seed production to be negatively related with STS transition because of increased strength of NDD effects, and longer exposure to mortality hazards prior to seedling censuses. Instead, we found contrasting responses between lianas (positive) and trees (negative). Thus, temporal concentration of seed rain suggested an effect of NDD in trees (see below) but not in lianas. The timing of seed production relative to the seedling censuses could account for this difference (i.e. if lianas and trees tended to produce most seeds shortly before and after seedling censuses, respectively). However, the timing of seed production was not consistent across years and some abundant trees also exhibited fruiting peaks shortly before census periods (e.g. *Dacryodes excelsa*, *Ocotea leucoxylon*). We conclude that the observed differences between life-forms are unlikely to be fully explained by phenological differences in seed production.

We found a negative effect of conspecific seed density on STS transition probability for trees. Intraspecific seed density has previously been shown to have negative effects on seedling survival in the LFDP (Comita *et al.* 2009) and in other forested systems (Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002). For tropical tree seedlings, mechanisms of negative density dependence other than competitive effects (i.e. Janzen-Connell effects) are probably most important (Paine *et al.* 2008). Neither conspecific nor heterospecific seed density had a significant effect on STS transition for lianas.

Abiotic drivers

Consistent with numerous other studies that have demonstrated strong effects of leaf litter on seedling emergence (e.g. Guzman-Grajales & Walker 1991; Everham, Myster & VanDeGenachte 1996; Sayer 2006; Dupuy & Chazdon 2008), we found a significant negative effect of leaf litter biomass on STS transition that was significant for lianas. The lack of a significant effect for trees may indicate that our leaf litter biomass data do not accurately capture among year variation in leaf litter input to seedling plots. Another possible explanation for the lack of a direct effect on trees is that species differ in their response to leaf litter conditions. In fact, we found a significant interaction between leaf litter biomass and seed size, which we discuss in the following section.

We expected light to have a positive direct effect on STS transition because it is an essential resource for plants and can also act as a germination cue (Swaine & Whitmore 1988; Vazquez-Yanes *et al.* 1990). In contrast, we found no direct effect of light on STS transition for either life-form. An interactive effect between light and leaf litter conditions could obscure this relationship. It is also possible that high seed or seedling mortality in plots with very high-light levels (i.e. canopy gaps) contributed to this result through desiccation. However, in their community-level analysis in the LFDP, Comita *et al.* (2009) found a positive effect of light on seedling survival only shortly after a hurricane, where the degree of canopy openness was substantially higher than the levels recorded in this study. After the canopy closed (i.e. 4–6 years following a major hurricane), factors other than light (e.g. conspecific seedling density, seedling height) were likely more important drivers of seedling survival.

We hypothesized that larger-seeded species would have higher overall STS transition rates but abiotic conditions would interact with this trait to modulate the STS transition (Moles & Westoby 2006). Specifically, we expected that STS transition of small-seeded species would be influenced positively by light and negatively by leaf litter relative to large-seeded species. Concordantly, we found a significant interaction between seed size and leaf litter biomass on STS transition probability for trees. Large-seeded tree species exhibited higher STS probabilities in plots with high leaf litter biomass, possibly reflecting lower seed predation or reduced desiccation (Sayer 2006). In contrast, high levels of leaf litter biomass reduced STS transition probability for small-seeded species that might have been buried without the resources to successfully germinate, root or reach a higher-light environment (e.g. Sayer 2006; Dupuy & Chazdon 2008). Previous research in the Luquillo forest found a negative effect of leaf litter for four species, including the large-seeded tree, *Dacryodes excelsa* Vahl (Guzman-Grajales & Walker 1991). Guzman-Grajales & Walker (1991) mimicked litter inputs immediately following a major hurricane (Hugo), which exceeded the total annual litter input during baseline years (Lodge *et al.* 1991). Our study represents variation in litter input over a 'normal' year as opposed to a single experimental simulation of a severe disturbance.

We found no evidence of an interaction between light conditions and seed size on the STS transition. The smallest-seeded species in our study were the pioneers (*Cecropia schreberiana*, *Schefflera morototoni* and *Alchorneopsis floribunda*), all of which are categorized as 'high-light regenerators' (Devoe 1989). The relatively large seeded, late successional trees included in this study are considered shade-tolerant and their seedlings can survive for long periods in closed canopy forests (Devoe 1989). Leishman & Westoby (1994) found that large seeds enjoy an advantage over small seeds most evident in extreme shade conditions (95–99%) because of larger initial energy reserves and higher growth rates. It is possible that relative small range of light levels throughout the plot were not sufficient to reveal differential responses of individual species.

Despite the extensive body of research on the ecological and evolutionary consequences of interspecific variation in seed size, the germination and establishment biology of lianas, in our study site and elsewhere, remain understudied. Additional research should examine variation among life-forms in germination success and the conditions influencing germination of lianas. It is possible that we did not find evidence of interactions between seed size and environmental conditions for this group because the range of seed size for the lianas in this study was relatively narrow (compared to trees) even though seed size of the five lianas included here spanned two orders of magnitude (0.051–0.395 g).

Conclusions

Exploring the ecological correlates of variation in seed size has received a tremendous amount of theoretical and empirical attention. This is because seed size is assumed to modulate critical ecological processes (i.e. fecundity, dispersal, competitive ability and stress tolerance) relevant to community dynamics and the maintenance of species diversity (Coomes & Grubb 2003; Muller-Landau 2010). Our results from the LFDP support the role of seed size in modulating some aspects of the STS transition in tropical forests. Seed size alone, however, may not capture many differences among species in their response to the environmental conditions that limit establishment, particularly in cross-site comparisons.

Some caveats to our results bear discussion. First, seed production in tropical forests can vary substantially across years (Norden *et al.* 2007a,b) and the effects of NDD can vary depending on the overall seed production (Wright *et al.* 2005). Because the data set analysed for this study spans only three years, we are unable to rigorously explore temporal variability in seed rain or the STS transition. Additionally, variation among species in their ability to persist in the seed bank likely contributes to variation in observed STS transition (Dalling *et al.* 2011). Second, Puerto Rico lacks a large native vertebrate fauna that, in other tropical forests, can play a key role in seed dispersal and seed predation. Additionally, particular disturbance regimes are likely to influence species composition in complex ways that cannot be fully captured by one study. Additional information on various biotic hazards governing the STS transition including post-dispersal seed predation, pathogen attack and seedling herbivory could provide valuable insight. These processes are variable in time and space and their roles in early life stage transitions of plants remain to be synthesized in terms of life-history trade-offs. Fortunately, long-term data sets appropriate for addressing these issues are becoming increasingly available (e.g. through the Centre for Tropical Forest Science [CTFS] network). Our study demonstrates the utility of using long-term field data to address fundamental questions about life-history trade-offs in plant communities.

Acknowledgements

This work was supported by NSF grants DEB-0516066 and DEB-0614659, which supported tree and seed/seedling censuses, respectively, and grants DEB-0620910 and DEB-0218039 from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, working with the International Institute of Tropical Forestry (USDA Forest Service), for the Luquillo Long-Term Ecological Research Program. The US Forest Service and the University of Puerto Rico provided additional support. Many thanks to the numerous members of seedling survey field crews and the El Verde field station technicians Marṍa Aponte, John Bithorn, Samuel Matta, José Rivera, Nereida Ramirez, Rebecca de Jesus and Paola Olaya for their data collection efforts. This manuscript was improved by comments of the editors and several referees. The authors have no conflict of interest to declare.

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Received 6 January 2012; accepted 22 October 2012
Handling Editor: Pieter Zuidema

Supporting Information

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

Appendix S1. Details of excluded observations.

Appendix S2. Null model of seed and seedling limitation.

Table S1. Explanatory variables used in the various models with observed ranges.

Table S2. Observed and randomized seed limitation and seedling establishment limitation for 19 species in the LFDP.

Table S3. Summary statistics for ANOVA's.

Figure S1. The Luquillo Forest Dynamics Plot and seed trap locations.

Figure S2. Cumulative proportion of total seeds collected from each of the 19 focal species and the grand total between August 2006 and May 2010.