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LETTER

Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest

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Abstract

Understanding demographic transitions may provide the key to explain the high diversity of tropical tree communities. In a faunally intact Amazonian forest, we compared the spatial distribution of saplings of 15 common tree species with patterns of conspecific seed fall, and examined the seed-to-sapling transition in relation to locations of conspecific trees. In all species, the spatial pattern of sapling recruitment bore no resemblance to predicted distributions based on the density of seed fall. Seed efficiency (the probability of a seed producing a sapling) is strongly correlated with distance from large conspecific trees, with a > 30-fold multiplicative increase between recruitment zones that are most distant vs. proximal to conspecific adults. The striking decoupling of sapling recruitment and conspecific seed density patterns indicates near-complete recruitment failure in areas of high seed density located around reproductive adults. Our results provide strong support for the spatially explicit predictions of the Janzen–Connell hypothesis.

Keywords

Amazonia, distance dependence, host–pathogen interactions, Janzen–Connell hypothesis, negative density dependence, ontogenetically integrated, Peru, regeneration dynamics, seed dispersal, tropical forest.

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INTRODUCTION

A number of studies over the past three decades have examined regeneration dynamics in tropical forests using large inventories of stems ≥ 1 cm diameter (Hubbell 1979; Wills *et al.* 1997; Hubbell *et al.* 1999; Condit *et al.* 2000; Peters 2003). These studies have greatly enriched our knowledge of tropical forest community ecology. Nevertheless, exclusive focus on stems ≥ 1 cm diameter overlooks processes occurring at the earliest life history stages because the majority of lowland tropical forest saplings ≥ 1 cm diameter are estimated to be at least 20 years old (Weldon *et al.* 1991; Hubbell 2004). Other studies, mostly unrelated to those cited above, have focused on early life history stages (Webb & Peart 1999; Queenborough *et al.* 2007, 2009; Metz *et al.* 2008; Comita & Hubbell 2009; Comita *et al.* 2010) and provided further insights. Yet, very few studies (Harms *et al.* 2000; Wright *et al.* 2005; Norden *et al.* 2007) have examined demographic transitions across life stages for multiple species. Meanwhile, most efforts to quantify seed fall in tropical forests through the use of seed traps were nearly all originally designed to study phenology, rather than sapling recruitment and are spatially extensive rather than intensive (Harms *et al.* 2000; Wright *et al.* 2005). Consequently, some of the most widely debated hypotheses related to tree recruitment processes and patterns in tropical forests remain inadequately tested in terms of spatially mapping demographic transitions across life stages. These include the Janzen–Connell (J–C) hypothesis (Janzen 1970; Connell 1971) and negative density dependence (NDD) (Hubbell *et al.* 1990; Condit *et al.* 1994; Wright 2002).

The J–C hypothesis predicts that recruitment patterns of tropical tree species are skewed away from parent trees, more specifically from areas of high seed density under/near the crowns of reproductive adults. In its original form, the model explicitly links together multiple life stages – seed fall and short-term seed/seedling survival, and the long-term time-integrated outcome as demonstrated by sapling cohorts that are displaced away from parent trees. Most spatially explicit tests of this prediction, however, have examined a single life stage using either seed, seedling or sapling cohorts (Janzen 1972; Augspurger 1984; Condit *et al.* 1992), and the few studies that span multiple life stages are typically of a single focal species and at most of several months duration (Clark & Clark 1984; Howe *et al.* 1985; Zuidema *et al.* 2002). The long-term time-integrated spatial predictions of the J–C hypothesis remain inadequately tested in an appropriate manner. Here, we report results from a long-term ontogenetically integrated study of tree recruitment patterns in a faunally intact Amazonian forest. We used 5 years of seed fall data collected in a high-density array of seed traps and contemporaneous sapling recruitment data to examine recruitment transitions across life stages over a contiguous forest stand. We compared the spatial distributions of young saplings of 15 common tree species with patterns of conspecific seed fall, and examined the seed-to-sapling transition in relation to locations of large conspecific trees.

MATERIAL AND METHODS

Data collection

Study site

Our research was conducted within a long-term forest dynamics plot in a faunally intact mature floodplain forest at Cocha Cashu Biological Station (CCBS, 71°24′21″ W, 11°53′15″ S), situated in the core region of Manu National Park in the Amazon headwaters region of southeastern Peru. The site is well-known for high biological diversity and an intact vertebrate community (Gentry & Terborgh 1990). The central hectare of the plot was originally established in 1974, and later expanded to 4 ha (200 × 200 m). All stems ≥ 10 cm d.b.h. are tagged, mapped and identified to species. Since establishment, the plot has been recensused regularly at 5-year intervals. At the most recent census conducted in 2005, the plot contained 2314 stems ≥ 10 cm d.b.h., representing > 300 species.

Seed fall data

In September 2002, a seed trap grid was established within the 120 × 120 m core of the long-term forest dynamics plot. The grid is comprised of 289 evenly spaced seed traps arranged in 17 rows and columns, each separated by 7.5 m (see Appendix S1 in Supporting Information). Each trap consists of a 0.5-m^2, open-topped, 1-mm nylon mesh bag stitched to a metal wire frame and suspended *c.* 1.2 m above the ground by tying the corners with fishing line to neighbouring trees. Traps are collected year-round on a bi-monthly schedule, and all fruits, seeds and fruit parts such as valves, pods, etc. falling into the traps are counted and identified to species.

For the analyses, we use seed fall collected over a 58-month span from September 2002 to July 2007. Analyses were restricted to all 'potentially viable propagules' (referred to simply as 'seeds' from here on) at the time of collection, a category that includes intact seeds without any visible damage (e.g. holes from bruchid beetles, rodent bite marks, etc.) and ripe, uninfested fruits. Fruits and seeds with obvious signs of infestation or damage at the time of collection were not considered in order to focus on post-dispersal seed fate, as well as eliminate any potential confounding effects caused by the sampling protocol.

Sapling recruitment data

Since 1997, sapling recruitment has been monitored in the core 90 × 90 m region of the forest dynamics plot, with regular recensuses at 4–5 years intervals. All stems ≥ 1 m tall and < 10 cm diameter are tagged, mapped and identified to species, a total of 8572 stems at the most recent recensus in 2006. For the analyses, only the youngest sapling cohort (stems ≥ 1 m tall, < 1 cm diameter) that recruited into the stand in that size class between 1997 and 2006 was used to minimize the temporal disjunction between

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seed fall and sapling recruitment data. While it is likely that the majority of saplings even in the youngest cohort arose from seeds that predated seed fall monitoring, most of these are likely to be < 20 years old as they measure < 1 cm in diameter (Weldon *et al.* 1991; Hubbell 2004). A comparison of the current composition of the forest stand within the central portion of the tree plot with that of past stand records (dating back to 1974) confirms that in most focal species, the same large, reproductive adults that are currently producing the bulk of the seed crop were present when current sapling recruits are likely to have arisen from seeds. Hence, patterns of contemporary seed fall are likely to closely resemble the seed fall patterns that produced saplings that are currently ≥ 1 m tall and < 1 cm diameter, which allows the direct comparison of contemporaneous sapling recruitment and seed fall patterns.

Analyses

We restricted analyses to 15 common canopy and sub-canopy tree species (Table 1) with sufficient sample sizes of seed fall (≥ 100 seeds), sapling recruits (≥ 10 individuals) and large trees (≥ 1 individual). The following procedures were performed individually for each species:

Seed fall data from the seed trap grid were used to estimate seed density across the entire grid surface using a simple Inverse Distance Weighting interpolation algorithm in ArcGIS 9.1 (ESRI 2005), based on actual numbers of seeds captured in the traps over the 58-month period. The search radius for the interpolation was restricted to the four nearest seed traps and the influence of surrounding seed traps on the interpolated value of seed density at any point within the grid was controlled by using a power value of 2 as the exponent of distance, which more strongly weights the nearest neighbour seed trap than linear interpolation. Estimated seed density values were outputted as 1 m^2 cells for the total area within the seed trap grid (120 × 120 m) and then clipped down to the 90 × 90 m (8100 m^2) central portion of the tree plot within which saplings have also been tagged and identified.

The estimated seed density surface was reclassified into seed density zones based on the seed density values of the 8100 1 m^2 cells. The lowest seed density zone was < 1 seed m^{-2} for all species, and subsequent zones were classified based on an approximately logarithmic series. Aggregate numbers of seeds in each seed density zone were tallied by sampling the original seed density surface using the zones defined by the reclassified surface. A digitized sapling stand map was created using the XY coordinates of saplings within the 90 × 90 m central area of the tree plot, overlaid on the reclassified seed density surface and the number of saplings located within each reclassified seed density zone was tallied.

Comparing seed fall vs. sapling recruitment patterns

We first examined the spatial distributions of sapling recruits in relation to the density of contemporaneous seed fall, without explicitly considering the locations of large conspecific trees. We tested an 'all seeds are equal' null hypothesis by comparing the observed distribution of saplings with the distribution expected if sapling recruitment patterns were to reflect seed density patterns. Aggregate seed numbers in each seed density zone were divided by the aggregate seed number in all seed density zones combined to obtain 'weights' for each seed density zone based on their relative contribution to the overall seed rain, i.e. $\Sigma(\text{weights}) = 1$. These weights were then multiplied by the total number of saplings to obtain an 'expected' number of saplings in each seed density zone based on the simple assumption that if all seeds are equal, sapling density should be directly proportional to seed density. The expected distribution of saplings in each density zone was compared to the observed sapling distribution using a chi-square test of distributions (Sokal & Rohlf 1995).

Effect of large conspecific trees on seed-to-sapling transition

We explored the effect of large conspecific adults on the seed-to-sapling transition by using simple proxy variables for seed efficiency or recruitment potential, i.e. the potential of a seed to eventually produce a sapling recruit > 1 m tall. Distance to nearest large conspecific tree (stems ≥ 10 cm d.b.h. for understory species and ≥ 30 cm d.b.h. for canopy species) was calculated for each square metre within the 200 × 200 m tree plot using the Spatial Analyst feature in ArcGIS 9.1. Calculated distance surfaces were then clipped to conform to the 90 × 90 m sapling plot, and clipped distance surfaces were reclassified into distance zones initially in increments of 5 or 10 m. Distance zones represented by < 100 m^2 were combined with a neighbouring zone so that every distance zone used in subsequent analyses covered at least 2.5% of total area (see Table S1 in Supporting Information).

Total number of seeds was tallied for each distance zone by sampling the original interpolated seed density surface (1 m^2 seed density estimates) using the zones defined by the reclassified distance surface. Total number of saplings located within each distance zone was tallied by overlaying the digitized sapling stand map on the reclassified distance surface. Sapling tallies were divided over the total number of seeds for each distance zone to obtain a sapling/seed ratio (SSR) for each distance zone.

For each species, SSR values were used to create two metrics that summarized the effect of distance from large conspecific trees on the seed-to-sapling transition. Net Seed Efficiency Gain (NSEG) was calculated as the multiplicative increase in the SSR between the farthest and nearest distance zones (i.e. $SSR_{\text{farthest}}/SSR_{\text{nearest}}$). $D_{50\%}$ was calculated as the distance (m) at which SSR reached half its maximum value. To compare across species of varying adult stature, $D_{50\%}$ values were also expressed as crown radius units (CRU) by dividing the raw $D_{50\%}$ value for each species by its mean crown radius (m). Based on the predictions of the J–C model, we would expect a large increase in seed efficiency in areas far from vs. near conspecific adults, which would produce a correspondingly large NSEG value and a $D_{50\%}$ value equivalent to multiple CRU. Mean crown radius values of the focal species were based on scaled photographs of entire trees whose crowns were fully visible along eroding river banks (Terborgh & Petren 1991). These values were comparable with crown radius measures of a few individuals of each focal species in the tree plot based on the average of the distance from trunk base to tip of the outermost branch in each of the four cardinal directions.

To examine whether the effect of large conspecific trees on seed efficiency is distinct from heterospecific trees, we also computed SSRs for each species with respect to the distance zones represented by large trees of each heterospecific species, one species combination at a time, and calculated the NSEG in each case. As the average crown radius of the 15 focal species varied considerably (1.3–8 m), the comparable farthest distance zone of all species was based on equivalent CRU rather than raw distance values. For example, for a species with a mean crown radius of 10 m whose farthest distance zone was 30–40 m, the comparable farthest distance zone for a species with a mean crown radius of 5 m would be 15–20 m. A total of 225 NSEG values were thus computed, based on 15 × 15 species combinations, representing 15 conspecific NSEG values and 210 heterospecific values (one 'conspecific NSEG' and 14 'heterospecific

Table 1 Net Seed Efficiency Gain (NSEG) and $D_{50\%}$ values for 15 common tree species

Family	Species	Trees	Saplings	Primary disperser	NSEG*	$D_{50\%}$† (m)	CR‡ (m)	$D_{50\%}$† (CRU)
Calophyllaceae	*Caraipa densifolia* Mart.	21	66	Wind	148.9	16.5	4	4.1
Lauraceae	*Caryodaphnopsis fosterii* Van der Werff	4	29	Bird	493.7	28.5	8	3.6
Cannabaceae	*Celtis schippii* Standl.	18	14	Bird	7.1	13	4	3.3
Putranjivaceae	*Drypetes amazonica* Steyerm.	27	23	Large primate	38.2	27	4.8	5.6
Annonaceae	*Dugetia quitarensis* Benth.	34	20	Small primate	2570.2	25.5	3	8.5
Violaceae	*Leonia racemosa* Ruiz & Pav.	21	44	Small primate	13.4	17	3	5.7
Salicaceae	*Lunania parviflora* Spruce ex Benth.	38	10	Bird	13.6	17	1.3	13.1
Annonaceae	*Oxandra sphaerocarpa* R. E. Fries	16	110	Bird, primate	3.1	5	2.9	1.7
Annonaceae	*Oxandra espintana* Baill.	16	24	Bird, primate	74.8	16	4	4.0
Moraceae	*Pseudolmedia laevis* J.F. Macbr.	50	59	Large primate	18.2	11.5	4.2	2.7
Malvaceae	*Quararibea wittii* K. Schum. & Ulbr	169	187	Small primate	4.4	8.5	3.2	2.7
Annonaceae	*Ruizodendron ovale* Ruiz & Pav.	34	13	Large primate	Infinity§	27.5	1.9	14.5
Malvaceae	*Theobroma cacao* L.	75	28	Large primate	29.8	17	1.8	9.4
Meliaceae	*Trichilia pleeana* C. DC.	11	36	Bird	32.4	39.5	3.1	12.7
Meliaceae	*Trichilia poeppigii* C. DC.	29	65	Bat	63.6	26	2.7	9.6
	Median				32.4	17.0		5.6

*Multiplicative increase in sapling/seed ratio (SSR) between nearest and farthest distance zones.

†Distance at which SSR = ½ NSEG, expressed in metres and crown radius units (CRU).

‡Average crown radius of large trees (see Material and methods for details).

§SSR was zero at the nearest distance zone (non-zero seeds and zero saplings).

Table 2 Comparison of models fitted with different functional forms for relativized data on sapling/seed ratio vs. distance of 15 common tree species

		Best fit parameter values			
Function	Form*	a	b	AIC	Delta AIC
Modified logistic	y = 1/(1 + (x/b)^a)	−1.722	5.669	32.38	0
Logarithmic	y = a*log(x)	0.296	NA	32.53	−0.15
Power	y = b*(x^a)	0.795	0.110	33.52	−1.14
Linear	y = ax + b	0.063	0.049	34.80	−2.42
Exponential	y = a*(exp(b*x))	0.209	0.101	42.18	−9.8
Null model	y = 0.39†	NA	NA	67.27	−34.89

*y = sapling/seed ratio; x = distance from nearest large conspecific tree (see Material and methods for details).

†Mean value of y in a null model representing no effect of distance.

NSEGs' for each species). For any given species, if the effect of large heterospecific trees on seed efficiency is equivalent to that of conspecific trees, we would expect to observe comparable NSEG values, on an average, for the 14 combinations of SSR vs. distance from large heterospecific trees in comparison to SSR vs. distance from large conspecific trees. Conversely, if the effect of large trees on seed efficiency is species-specific (as postulated in the J–C hypothesis), NSEG of a species in relation to large conspecific trees would typically be much larger than the NSEG with respect to large heterospecific trees.

Empirically derived 'escape' curve

The theoretical 'escape' curve of the J–C model (figure 1 in Janzen 1970) depicts the probability that a seed or seedling will mature as: zero or extremely low in the vicinity of parent trees, increasing sharply beyond a certain intermediate distance and levelling off at farther distances. We modelled a multi-species 'escape' curve by using SSR values of all 15 species as a proxy for survival probability/recruitment potential. Raw SSR values had to first be relativized across species because their ranges differed amongst species by as much as two orders of magnitude due to interspecific differences in fecundity. Therefore, for each species, SSR values of each distance zone were divided by the largest SSR value to obtain a set of values between 0 and 1. Raw distance values also had to be relativized across species because average crown radii of the 15 focal species varied considerably (1.3–8 m). Therefore, median distance values of distance zones for each species were divided by the mean crown radius (m) to obtain distance measures in terms of CRU. The pooled set of relativized SSR values of all 15 species were plotted against their corresponding relativized distance values and fitted with a modified form of the logistic growth equation (Table 2), which closely approximates the shape of the theoretical 'escape' curve. Additionally, for comparison, we fitted the data to a null model representing no effect of distance, and to other common functional forms (linear, power, exponential and logarithmic). Model-fitting and parameter optimization was performed in the statistical software package R (R Development Core Team 2008), using the 'nls' function. Model fits based on different functional forms were compared with computed AIC values.

RESULTS

Seed fall vs. sapling recruitment patterns

In all 15 species examined, actual distributions of saplings bore no resemblance to expected distributions based on seed density: areas of highest seed density corresponded with areas of lowest sapling recruitment and *vice versa*, and the expected vs. observed sapling distributions were a complete mismatch in most cases (Figs 1 and 2). Saplings of all 15 species recruited in areas of lowest seed density at much higher abundances than predicted by an 'all seeds are equal' null hypothesis, and areas of highest observed number of saplings corresponded with lowest predicted numbers of saplings.

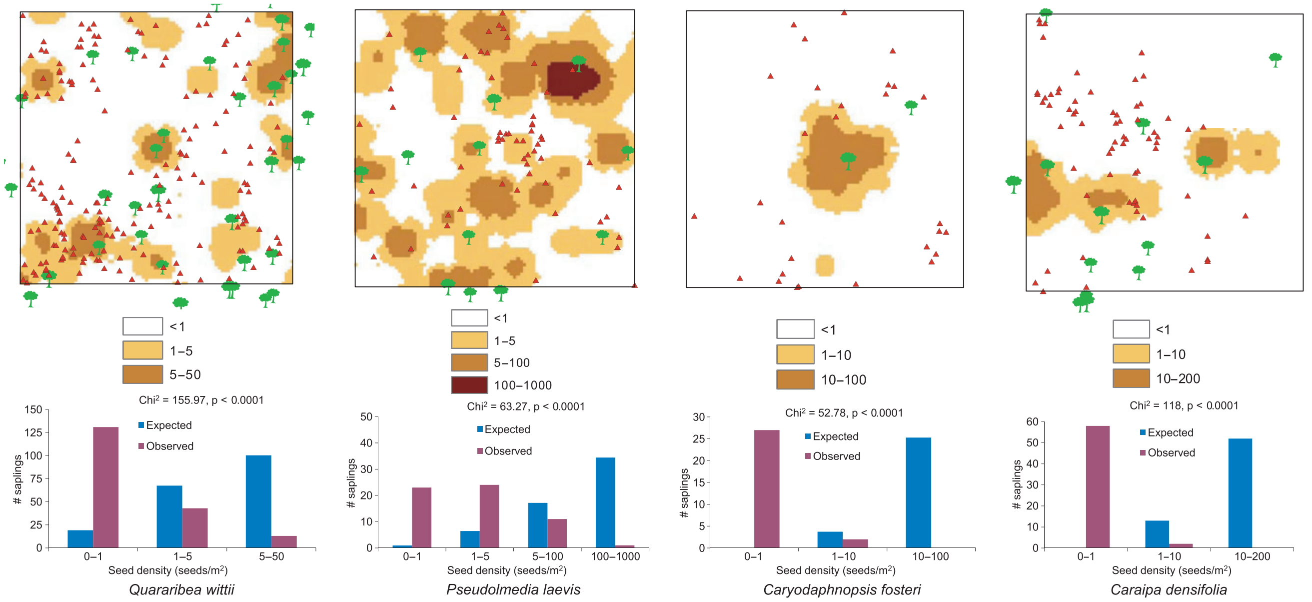
Effect of large conspecific adults on seed-to-sapling transition

Net Seed Efficiency Gain values ranged from 4.4 to 2570.2 with a median value of 32.4 (Table 1). $D_{50\%}$ ranged from 5 to 39.5 m with a median value of 17 m. Expressed in CRU, $D_{50\%}$ ranged from 1.7 CRU to 14.5 CRU with a median value of 5.6 CRU. In all 15 species, NSEG values in relation to large conspecific trees were almost unanimously much larger (typically by orders of magnitude) than NSEG values in relation to large heterospecific trees (see Table S2 in Supporting Information). Of the 196 possible comparisons of conspecific vs. heterospecific NSEG values (14 comparisons for each species), a heterospecific value was greater than the conspecific value in only a single instance ($< 1\%$).

A model based on a modified logistic function provided the best fit for the pooled set of relativized SSR values of all species plotted against their corresponding relativized distance values (Table 2; Fig. 3). A model based on a logarithmic function provided an equivalent fit, which was substantially better than models based on power, exponential and linear functions. All functional forms were a significant improvement over a null model representing no effect of distance.

DISCUSSION

Our results suggest that sapling recruitment patterns in tropical forests are largely decoupled from the distribution of conspecific seed fall. The near-total recruitment failure observed in the areas of highest conspecific seed density supports the widely reported phenomenon of negative density dependence (NDD) in tropical forests



Quararibea wittii *Pseudolmedia laevis* *Caryodaphnopsis fosteri* *Caraipa densifolia*

Figure 1 Observed vs. expected distribution of saplings in relation to conspecific seed fall distribution, with corresponding test statistics and stand maps for four common tree species. Green tree symbols represent stems > 10 cm d.b.h., with size scaled according to d.b.h. Red triangles represent saplings (stems ≥ 1 m tall, < 1 cm diameter). Seed density classes (seeds m^{-2}) are shaded from white to dark-brown, representing regions of lowest to highest estimated seed densities, respectively. The entire extent of the 200 × 200 m tree plot is not shown in the figure, only the central 90 × 90 m region in which saplings have also been mapped. In some cases, large trees located within 5 m outside the central 90 × 90 m area are also shown.

(Wright 2002). The spatially explicit analyses presented here illustrate that density-dependent recruitment patterns are spatially non-random because the regions of highest seed density that experience near-complete recruitment failure are invariably in the vicinity of conspecific trees. Large values of NSEG and $D_{50\%}$ in relation to conspecific trees (whether measured in metres or CRU) for most individual species provide convincing support for the influence of large conspecific adults on the seed-to-sapling transition. The empirically derived 'escape' curve fitted to the pooled species data (Fig. 3) indicates that, on an average, the inhibitory effect of conspecific adults on seed efficiency extends out to several multiples of crown radii and begins to level off only beyond a distance of *c.* 10 CRU. Density-dependent recruitment in our study species is thus strongly and explicitly distance dependent as well.

Our results also illustrate that the effect of large trees on seed efficiency is strongly species-specific, with conspecific trees exerting a powerful negative influence on the seed-to-sapling transition whereas heterospecific trees have minimal effect. Species-specific NDD in tropical forests has been previously documented for the seedling life stage (Comita & Hubbell 2009; Comita *et al.* 2010). Here, we show that the seed-to-sapling transition, which encompasses the seedling life stage, is characterized by the overcompensating form of density dependence (Bagchi *et al.* 2010). Recruitment failure in the vicinity of large trees could also result from resource limitation via asymmetric competition between large adult trees and early life stages (Lewis & Tanner 2000). However, the strong species specificity of our results and the absence of a general negative effect of large trees on the seed-to-sapling transition suggest a minimal role for asymmetric competition in the pronounced spatial patterning of the demographic transition across early life stages.

Our study design does not directly provide a mechanistic basis for the observed pattern of NDD in the seed-to-sapling transition. Our findings therefore might be interpreted as prima facie evidence for either of two different mechanisms, each produced by entirely different processes: intracohort resource competition as a result of intratrophic interactions, or intertrophic interactions between plants and their natural enemies, as postulated by the J–C hypothesis. However, there is scant evidence in support of intraspecific resource competition playing an important role in the regeneration dynamics of tropical forests, especially at early life stages. Multiple recent experimental studies from different tropical forests (Paine *et al.* 2008; Svenning *et al.* 2008) have confirmed that intracohort interactions are weak and play a negligible role in survival and establishment of early life stages. In contrast, rapidly accumulating evidence from experimental studies suggests that our findings are consistent with the processes described by the J–C hypothesis, i.e. intertrophic interactions between plants and their natural enemies, which causes overcompensating density-dependent mortality of early life stages in the vicinity of conspecific trees (Bell *et al.* 2006; Bagchi *et al.* 2010). Through a long-term experiment conducted at the same study site (Swamy & Terborgh 2010), we found strong, multi-species support for the influence of distant-dependent, host-specific natural enemies on seedling establishment patterns, and no evidence for intraspecific (or interspecific) resource competition, even under artificially fixed, highly elevated seedling densities. A long-term study on the fate of naturally occurring seedling carpets of multiple species at this study site (P. Alvarez & J. Terborgh, unpublished data) confirms that natural enemies are primarily responsible for mortality of high-density cohorts of conspecific seedlings.

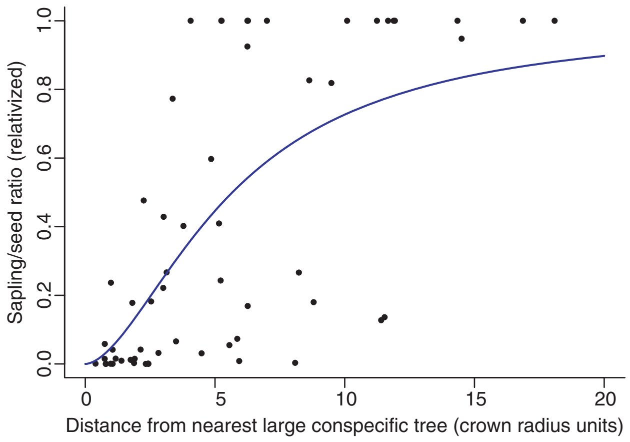


Figure 3 Relativized sapling/seeds ratio (SSR) values plotted against distance from nearest large conspecific tree (expressed in crown radius units) for 15 common tree species, fitted with a modified logistic function (see Materials and methods for details).

The long-term consequence of extremely low recruitment success of seeds that fall in the proximity of large conspecific trees is a spatial pattern where the nearest saplings of the majority of common species are located at distances equivalent to several crown-widths away from conspecific adult trees (Terborgh *et al.* 2002). Because our sampling protocol distinguishes between undispersed and dispersed propagules that comprise the seed fall data, we are also able to accurately map the distinct distributions of the undispersed and dispersed portions of the seed crop and compare these with the distribution of conspecific saplings. Results of this analysis (J. Terborgh, P. Alvarez, K.G. Dexter, F. Cornejo, C. Carrasco unpublished data) conclusively show that all seeds are

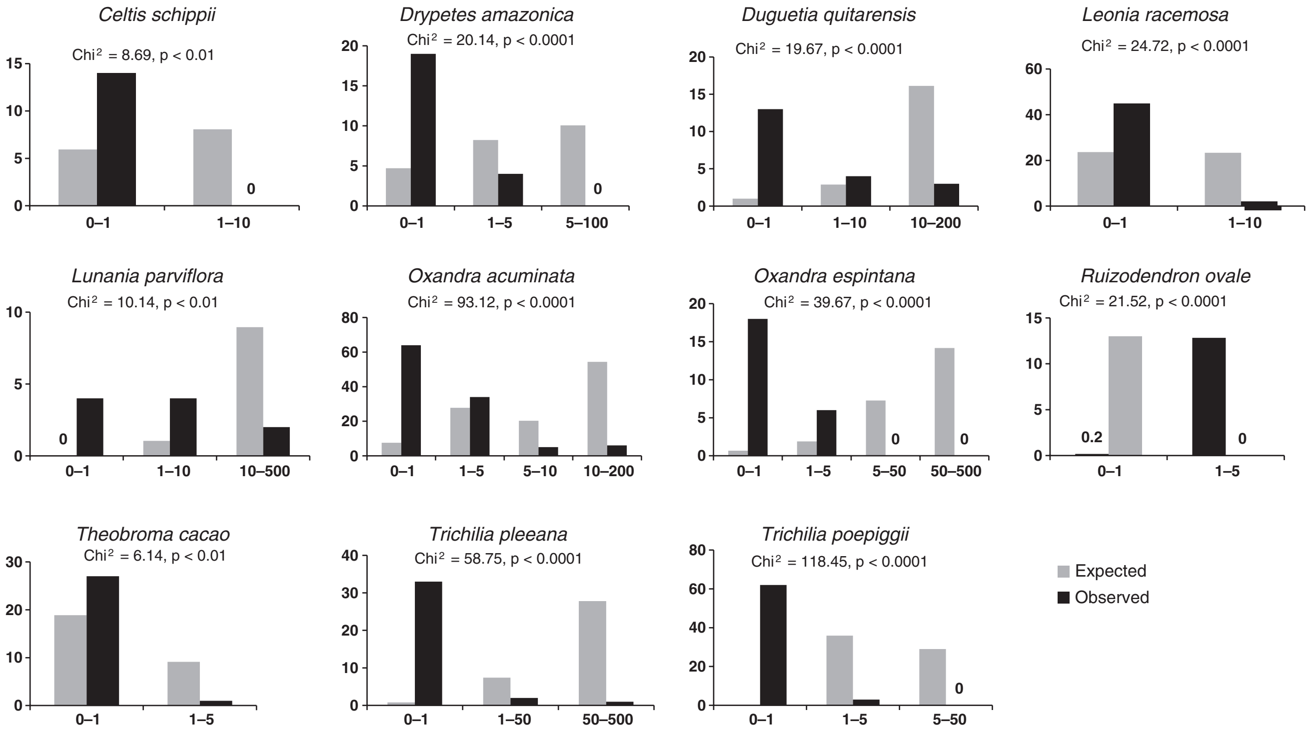


Figure 2 Observed (black bars) vs. expected (grey bars) distribution of saplings in relation to conspecific seed fall distribution, with corresponding test statistics for 11 common tree species. X-axis: seed density zones (seeds m^{-2}). Y-axis: number of saplings.

not equal – the overwhelming majority of saplings arise from seeds that are dispersed away from the crown zones of conspecific parent trees. Seed dispersal therefore appears critical for successful recruitment, and seeds that fall within/near the crown zones of reproductive adults make a minimal contribution to later life stages. The significance of near-complete failure of undispersed seeds is perhaps best demonstrated by examining recruitment patterns in the absence of zoochorous seed dispersal in an 'empty' forest lacking large vertebrate frugivores (Terborgh *et al.* 2008). The sharp drop in the species diversity of sapling recruits and the drastically altered community composition observed is perhaps the most direct support for the predictions of the J–C hypothesis relating to maintenance of alpha-diversity in tropical tree communities. From a conservation standpoint, it places a premium on seed dispersal services provided by large vertebrate frugivores that are the most favoured targets of hunters and have been eliminated from all but the most remote and well-protected tropical forests (Peres & Lake 2003; Peres & Palacios 2007).

To the best of our knowledge, this research is the first to report spatially and temporally concurrent measurements of seed fall and sapling recruitment of multiple species across a contiguous, faunally intact tropical forest stand over a multi-year period. Therefore, it provides the first multi-species ontogenetically integrated empirical support for the spatially explicit predictions of the J–C hypothesis across a forest stand. Since 2008, we have begun monitoring seed fall and sapling recruitment in two other faunally intact as well as three defaunated forest sites spread across the *c.* 80 000 km^2 Madre de Dios river basin in the lowland Amazon forests of southeastern Peru. Data from long-term ontogenetically integrated studies of forest regeneration processes will eventually provide a more complete understanding of the mechanisms that allow for species co-existence and spatial organization of hyperdiverse tropical forests, as well as the consequences of human-induced perturbations on these ecosystems.

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SUPPORTING INFORMATION

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

Appendix S1 Schematic of the ontogenetically integrated study design.

Table S1 Distribution, median distance and area covered by distance zones of the 15 focal species.

Table S2 NSEG values based on conspecific and heterospecific adults calculated for each of 15 focal species used in the study.

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