

Decomposing dispersal limitation: limits on fecundity or seed distribution?

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Summary

1. The term 'dispersal limitation' represents two distinct component processes: the number of seeds produced (fecundity) and the spatial pattern of the seed rain (distribution). We present a quantitative evaluation of these component processes of dispersal limitation for a tropical forest tree community.
2. Using a regularly spaced grid of 289 seed traps (0.5 m² each), we monitored the seed rain into 1.44 ha of upper Amazonian floodplain forest for 6 years whilst concurrently monitoring sapling recruitment in a 0.81-ha subplot centred within the seed-trapping grid. This arrangement allowed us to compare the spatial pattern of seed rain with that of sapling recruitment.
3. We endeavoured to distinguish between undispersed and dispersed seeds by applying a series of criteria to seeds collected in the traps and by removing from certain analyses all seeds that fell under reproductive conspecifics. Gross fecundity of 30 common species that contribute to the advanced regeneration was uniformly low and the rain of dispersed seeds was lower still, being < 1.0 m⁻² year⁻¹ in every case.
4. The rain of dispersed seeds with respect to conspecific reproductives closely matched the recruitment of saplings, whereas gross seed rain (all seeds, including undispersed seeds) did not.
5. *Synthesis.* 'Dispersal limitation' in this faunally intact Amazonian forest is primarily attributable to a scant rain of dispersed seeds, i.e. fecundity limitation, whereas the distribution of dispersed seeds, being random for most species, appears adequate. Evidence from this and earlier research at the same site indicates that the per-capita success of dispersed seeds is many times higher than that of undispersed seeds. Thus, seed dispersal kernels that do not distinguish between dispersed and undispersed seeds are likely to be biologically misleading.

Key-words: Amazon, determinants of plant community diversity and structure, dispersal limitation, fecundity, Perú, sapling recruitment, seed rain, tropical forest, winner by forfeit

Introduction

'Dispersal limitation' has become a major topic in the long-simmering discussion over the processes that maintain the high-tree diversity of tropical forests (Hubbell 2001; Chave, Muller-Landau & Levin 2002; Wright 2002). Dispersal limitation is defined as failure of the propagules of a given species to arrive at an available site. However, as subsequently pointed out by Muller-Landau *et al.* (2002) and Schupp, Milleron & Russo (2002), dispersal limitation operates through two

orthogonal processes: the production of propagules (fecundity) and the dispersion of propagules (distribution) over the area of interest. Here, we endeavour to achieve a full separation and analysis of the roles of these two component processes of dispersal limitation.

The distinction between fecundity and distribution is an important one. Other things being equal (seed size, proportion of seeds dispersed, etc.), fecundity is primarily a function of adult abundance. As most species in hyperdiverse tropical forests are rare by temperate standards, having less than 1 individual ≥ 10 cm d.b.h. per hectare (Pitman *et al.* 2001; Losos & Leigh 2004; Macia & Svenning 2005), one must assume that

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fecundity is strongly limiting for most species, a supposition that is supported by seed addition experiments (Svenning & Wright 2005; Clark *et al.* 2007). Nevertheless, much of the emphasis in discussions of dispersal limitation has been on the distribution parameter (Hubbell 2001; Muller-Landau *et al.* 2002, 2008). There is, however, a paradox here in that failure to distribute seeds widely (if sparsely) across available establishment sites would result in progressive clumping of populations. Although spatial aggregation of mature individuals appears to be a nearly universal property of tropical tree populations (Condit *et al.* 2000), there is no evidence that clumping of populations increases through time.

Dispersal limitation, whether via limited fecundity or non-uniform dissemination of seeds, can lead to the situation Hurtt & Pacala (1995) described as 'winning by forfeit'. 'The effect of recruitment limitation is that it permits inferior species to win sites in the absence of dominant competitors' (Hurtt & Pacala 1995, p. 2). Winning by forfeit is a variant of the competition-colonization trade-off, but in hyperdiverse tropical forests it involves essentially every species, so winning by forfeit goes beyond any simple dichotomy and does not depend explicitly on limitations of either fecundity or distribution (Muller-Landau 2008). To our knowledge, there has not been any previous attempt to quantify the winning by forfeit process in tropical forests.

We begin by comparing the fecundities of 30 common tree species that participate in the advance regeneration. The fecundities are low in every case, whether evaluated by an 'all seeds are equal' model or by a more exclusive model that emphasizes dispersed seeds. Next, using null models, we analyse the spatial distributions of the seed rain and of newly recruited saplings and show that both occur at random locations with respect to reproductive conspecifics. Finally, we comment on 'winner by forfeit' and show that it is pervasive at the scale of individual establishment sites but not at the much larger scale at which diversity is maintained in tropical forests. We conclude that dispersal limitation is overwhelmingly attributable to fecundity limitation and that the extremely low rain of dispersed seeds largely precludes a role for density dependence in establishment.

Materials and methods

GENERAL SETTING AND SITE HISTORY

The research was conducted in floodplain forest at the Cocha Cashu Biological Station in the Manu National Park, Madre de Dios, Perú (11°54' S, 71°22' W). With annual precipitation in the range of 2000–2500 mm, the site is classified as tropical moist forest under the Holdridge system. Relevant to this research is the fact that the animal community at Cocha Cashu is intact and all dispersers and seed predators are present at ecologically regulated densities. Further details are available in Gentry (1990) and Endo *et al.* (2010).

The 4-ha tree plot within which the measurements were carried out was established in 1974–1975 as a 1-ha plot (Gentry & Terborgh 1990). The plot was expanded in 1988–2.25 ha, and again in 2002 to its current size of 4 ha. All included trees ≥ 10 cm d.b.h. have been censused every 5 years since 1975, with the most recent census in 2005.

Meanwhile, in 1997–1998, nine centrally located 30×30 m subplots (0.81 ha) were sampled for saplings. All stems ≥ 1 m tall and < 10 cm d.b.h. (trees and treelets, but not lianas) were tagged, mapped, measured and identified following procedures described in Terborgh *et al.* (2008). We recensused all saplings in 2002 and 2006, documenting mortality, recruitment and survival, to give us a 9-year record of sapling dynamics to complement the 30-year record for trees.

MONITORING SEED RAIN

In 2002, we established a seed trap array to monitor fruits and seeds falling from the canopy. We use 0.5-m^2 traps constructed of fine mesh screening mounted on heavy wire frames and suspended from the four corners at a height of *c.* 1 m by lines attached to nearby vegetation. The 289 traps are arrayed 7.5 m apart in a square grid 120 m on a side, covering an area of 1.44 ha, the centre of which is occupied by the 0.81-ha sapling monitoring plot. Contents of the traps are collected, sorted and identified every 15 days. Unfamiliar seeds are identified with the aid of a reference collection of dried seeds initiated by F.C. in 1984 that currently contains over 600 taxa, including nearly all trees and lianas and most shrubs found in the plot. In addition, we maintain a reference collection of digital photos of fresh fruits and seeds of most taxa. For the purposes of this report, we used data collected from the initiation of the monitoring programme in September 2002 through September 2008, for a total of 6 years of collections.

A major objective was to collect data in a way that would allow us to achieve at least a partial separation of dispersed from undispersed seeds, because a substantial literature suggested that undispersed seeds, especially those contained in fruits and those with adherent pulp, suffer high mortality from vertebrate and invertebrate seed predators and fungi (e.g. Silvius & Fragoso 2002; Fragoso, Silvius & Correa 2003). Thus, we classified propagules (fruits and seeds) into the following categories: intact seeds, seeds with adherent pulp, damaged seeds, ripe fruit, immature and damaged fruit. We defined as 'intact' individual seeds that were clean of any adherent pulp and that lacked any evidence of predation (e.g. holes of bruchid beetles). We distinguished dispersed from undispersed seeds by determining, which seeds fell beneath the crown of conspecific fruiting adults using estimated crown diameters and a 'cookie-cutter' function in ArcGIS V. 9.3. By our system, most dispersed seeds are classified as 'intact', but not all intact seeds are dispersed, because some clean seeds are dropped beneath the parent tree by monkeys and other dispersers. Intact seeds that have been transported from other fruiting conspecifics can be regurgitated or defecated under a given reproductive conspecific. Overall, the proportion of 'intact' seeds that fell under the crowns of fruiting conspecifics was low (median 0.06).

MONITORING SAPLING RECRUITMENT

The main tree plot at Cocha Cashu is divided into 30×30 m subplots. The nine central subplots (0.81 ha) were selected for the monitoring of sapling recruitment and all saplings (≥ 1 m tall and < 10 cm d.b.h.) were tagged, measured, mapped and identified in 1997 and 1998. Saplings were recensused in 2002 and 2006 and all recruitment and mortality were recorded. In this report, the focus is on the recruitment of new saplings into the stand, so we shall use the word 'sapling' to refer to small saplings ≥ 1 m tall and < 1 cm d.b.h.

DETERMINATION OF REPRODUCTIVE STATUS

Approximately 900 trees ≥ 10 cm d.b.h. overhang the trap grid. With a trap every 7.5 m, most, but not all, fruit crops produced by

canopy-level trees are registered in the traps as fallen fruit or as undispersed fruit parts, such as the valves of legumes or dehiscent capsules (with certain exceptions noted below). Our 6-year record is sufficient to document which trees are reproductive and which are not, including dioecious species.

Several species were so efficiently dispersed that the traps captured only dispersed seeds, leaving us with no clues as to which individual trees had fruited. To correct for possible errors of omission in designating fruiting adults, each adult tree of the relevant species in and around the margins of the 1.44 ha covered by the trap grid was carefully inspected during the fruiting season of 2009.

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The intensity of the seed rain varies greatly across species. Seed mass and adult abundance explain only a fraction of this variation (J. Terborgh & P. Alvarez, unpubl. data), so other factors are clearly involved. We make no attempt to identify these other factors here.

Propagules falling close to fruiting adults only rarely produce saplings (Janzen 1970; Connell 1971), whereas dispersed seeds falling far from conspecifics enjoy much enhanced per-capita success (Howe, Schupp & Westley 1985; Terborgh *et al.* 2002; Terborgh & Nuñez-Ituri 2006). Thus, we shall recognize two representations of fecundity that we shall refer to as 'gross' and 'net'. Gross fecundity is the most commonly reported measure and carries the implicit assumption that 'all seeds are equal'. It includes all potentially viable seeds, represented as: (intact seeds + seeds with adherent pulp) + (ripe fruits \times no. seeds/fruit). Net fecundity includes only seeds that have been dispersed away from the parent tree and that met our criteria for 'intact' seeds (see above).

To place our results into the context of previous studies, we followed Clark, Macklin & Wood (1998) and Muller-Landau *et al.* (2002) in calculating standard descriptive statistics for each species: seed limitation, source limitation and dispersal limitation (Table 1). Seed limitation is the proportion of sites (traps) that failed to capture seeds; source limitation is the proportion of sites not reached by seeds if the observed seed rain was Poisson distributed; dispersal limitation is the proportion of sites actually reached relative to the proportion expected if dispersal had been Poisson distributed.

DISPERSION OF INTACT SEEDS AND SAPLINGS IN RELATION TO FRUITING ADULTS

A central goal of the research was to compare the spatial distribution of the seed rain to that of sapling recruitment with respect to fruiting conspecific adults. Only 17 species out of the 269 species with stems ≥ 10 cm d.b.h. in the 4-ha plot could be analysed because each one had to satisfy multiple criteria: attainment of reproductive maturity at ≥ 10 cm d.b.h., ≥ 5 fruiting adults in the plot, ≥ 5 recruited saplings and ≥ 15 dispersed 'intact' seeds over the 6-year period. (see Table 2). These criteria eliminated small-seeded gap colonizers, because saplings of these species are only rarely encountered in the advance regeneration, but obligate gap colonizers comprise only a few percent of the adult stand.

To determine if saplings were nearer to or farther from conspecific fruiting adults than expected by chance, we used a randomization approach. For each species, we maintained the actual number and location of fruiting adults and then randomized the location of saplings (using the observed number of saplings) within the 90×90 -m sapling plot. We repeated this randomization 2000 times and determined the median distance to the closest fruiting adult for each replicate. This gave a null distribution of median distances against

which to compare the observed value. Our simplistic null model could be biased if there were spatial structure in the distribution of saplings. However, visual analyses of sapling distributions did not reveal any evident patterns in distribution (e.g. clustering or overdispersion), thus obviating the need for more complicated null models that can preserve spatial structure present in distributions (e.g. John *et al.* 2007). We did not have a clear prediction as to whether saplings would be closer to or farther from fruiting adults than expected by chance, so we used a two-tailed test in this comparison (with a threshold *P*-value of 0.05). If fewer than 2.5% of the randomizations showed a median distance less than that observed in the real data, this would signify that saplings are found closer to fruiting adults than expected by chance. Conversely, if more than 97.5% of the randomizations showed a distance less than that observed, saplings would be further from fruiting adults than expected by chance.

In addition to species-level analyses, we assessed at the community level whether saplings were closer to or farther from conspecific fruiting adults than expected by chance. We used a paired *t*-test comparing the observed versus expected median distance to the closest fruiting adult for all 17 focal species. The expected value for each species is simply the mean of the median distance across all randomizations.

We conducted analyses for all small saplings (≥ 1 m tall and < 1 cm d.b.h.) that first appeared in the census in either 2002 or 2006. These saplings represent individuals that recruited into the plot since the first census in 1997 and are thus most appropriate for comparing to the concurrent seed rain. To ensure that results were consistent with larger sample sizes (several species had < 10 recruited saplings), we repeated analyses using all conspecific saplings (≥ 1 m tall to < 10 cm d.b.h.) that were recorded in the plot at any time between 1997 and 2006.

A similar approach was followed in assessing whether the seed rain was distributed at random with respect to fruiting adults. For a given species, we totalled the number of seeds that fell into each trap across all 6 years and then randomized the location of seed traps, ensuring that traps in randomizations were only allowed to occur at sites, where traps are present in the real data (i.e. maintaining the grid distribution). A critical aspect of these randomizations is that we preserved the real distribution of abundance of seeds in traps for each species rather than randomly distributing seeds across all traps. The latter approach would give an unrealistic, over dispersed distribution of seeds as the null model. We used seed totals corresponding to the two different scenarios of fecundity: 'gross', which includes all potentially viable seeds and 'net', which includes only dispersed, intact seeds (using the 'cookie-cutter' procedure mentioned above). Under both scenarios, we calculated the median distance to closest fruiting adult for all seeds for each randomization and compared it to that observed in the real data. Note that the units of randomization here are the seed traps, whilst the median distance is calculated across all individual seeds. We also compared the median distance to the closest fruiting adult of recruited saplings versus the median distance at which seeds fell for the 17 species for both the 'gross' and 'net' fecundity scenarios. Specifically, we asked if this relationship differed significantly from a 1:1 relationship by determining whether the slope differed significantly from 1.0 and whether the intercept differed significantly from 0 using *t*-tests (Sokal & Rolf 1995).

ELIMINATION OF BOUNDARY EFFECTS

An error in computing distances from seeds or saplings could arise when the nearest fruiting conspecific is located outside the 1.44-ha area in which seed rain was monitored. We took two steps to minimize these potential boundary effects. First, we used logistic regression on

Table 1. Gross and net fecundity of 30 species of canopy trees with seed weight, principal dispersal mode and dispersal parameters

Species	Seed dry mass (g)	Dispersal mode	Gross fecundity: seeds per m ² -year	Proportion of gross fecundity falling under crowns	Net fecundity: seeds per m ² -year	Net as proportion of gross	Seed limitation (net)	Source limitation (net)	Dispersal limitation (net)	Seed limitation (gross)	Source limitation (gross)	Dispersal limitation (gross)
<i>Agonandra brasiliensis</i>	1.12	Mam.	0.012	0.00	0.012	1.00	0.98	0.97	0.39	0.98	0.97	0.39
<i>Aspidosperma magaphyllum</i>	0.33	Wind	0.332	0.81	0.029	0.09	0.93	0.92	0.12	0.91	0.37	0.86
<i>Batocarpus amazonicus</i>	0.65	Mam.	0.196	0.04	0.191	0.97	0.75	0.56	0.43	0.74	0.56	0.42
<i>Brosimum alicastrum</i>	0.18	Mam.	3.467	0.95	0.256	0.07	0.83	0.46	0.68	0.70	0.00	0.70
<i>Carapa densifolia</i>	0.08	Wind	4.096	0.88	0.038	0.01	0.95	0.89	0.57	0.84	0.00	0.84
<i>Celtis schippii</i>	0.06	Bird	0.191	0.12	0.129	0.67	0.78	0.68	0.31	0.74	0.56	0.40
<i>Chrysophyllum venezuelanense</i>	0.81	Mam.	0.260	0.03	0.068	0.26	0.92	0.81	0.57	0.92	0.46	0.85
<i>Clarisia racemosa</i>	1.51	Mam.	0.982	0.82	0.182	0.19	0.71	0.58	0.32	0.56	0.05	0.54
<i>Dipterix micrantha</i>	1.23	Bat	0.089	0.74	0.015	0.17	0.96	0.96	0.15	0.82	0.77	0.25
<i>Drypetes amazonica</i>	0.23	Bird	0.216	0.72	0.039	0.18	0.95	0.89	0.55	0.89	0.52	0.76
<i>Hyeronima laxiflora</i>	0.01	Bird	56.205	0.99	0.254	0.00	0.83	0.47	0.69	0.74	0.00	0.74
<i>Inga chartacea</i>	0.12	Mam.	1.012	0.56	0.074	0.07	0.91	0.80	0.56	0.89	0.05	0.88
<i>Leonia glycyarpa</i>	0.21	Mam.	0.617	0.59	0.040	0.06	0.93	0.89	0.38	0.89	0.16	0.87
<i>Mabea maynensis</i>	0.08	Expl.	1.375	0.87	0.089	0.06	0.89	0.77	0.54	0.85	0.02	0.85
<i>Matisia cordata</i>	2.22	Mam.	0.189	0.26	0.122	0.64	0.84	0.69	0.47	0.79	0.57	0.50
<i>Nectandra longifolia</i>	0.39	Bird	0.050	0.00	0.048	0.98	0.90	0.86	0.28	0.90	0.86	0.27
<i>Otoba parvifolia</i>	1.16	Bat	0.427	0.72	0.092	0.22	0.84	0.76	0.34	0.70	0.28	0.58
<i>Oxandra acuminata</i>	0.25	Bird	0.678	0.33	0.355	0.52	0.67	0.35	0.50	0.62	0.13	0.57
<i>Oxandra espinhata</i>	0.09	Bird	1.014	0.62	0.230	0.23	0.76	0.50	0.52	0.72	0.05	0.70
<i>Pseudobmedia laevis</i>	0.11	Mam.	2.390	0.72	0.634	0.27	0.58	0.15	0.51	0.49	0.00	0.49
<i>Quararibea wittii</i>	0.23	Mam.	1.280	0.77	0.057	0.04	0.89	0.84	0.30	0.56	0.02	0.55
<i>Ruizodendron ovale</i>	0.79	Mam.	0.090	0.33	0.059	0.66	0.89	0.84	0.35	0.88	0.76	0.47
<i>Sorocea pileata</i>	0.18	Mam.	0.167	0.01	0.155	0.92	0.72	0.63	0.23	0.70	0.61	0.24
<i>Spondias mombin</i>	1.48	Mam.	0.734	0.87	0.062	0.08	0.90	0.83	0.39	0.80	0.11	0.77
<i>Theobroma cacao</i>	0.60	Mam.	0.360	0.33	0.018	0.05	0.95	0.95	0.10	0.91	0.34	0.86
<i>Trichilia plicata</i>	0.55	Bird	1.858	0.94	0.106	0.06	0.86	0.73	0.48	0.81	0.00	0.81
<i>Trichilia poeppigii</i>	0.39	Bat	0.482	0.80	0.055	0.11	0.93	0.85	0.52	0.89	0.24	0.85
<i>Virola calophylla</i>	0.55	Mam.	0.247	0.19	0.146	0.59	0.77	0.65	0.36	0.72	0.48	0.47
<i>Xylosma inermidia</i>	0.01	Bird	24.420	0.90	0.238	0.01	0.87	0.49	0.75	0.76	0.00	0.76
<i>Ziziphus chinanomum</i>	1.58	Mam.	0.044	0.13	0.033	0.75	0.95	0.91	0.48	0.90	0.88	0.16
Median	0.36	-	0.45	0.67	0.08	0.18	0.89	0.78	0.45	0.80	0.26	0.64

Table 2. Observed versus expected median distance to closest fruiting adult for recruited saplings and dispersed, intact seeds. The expected distance is the mean across 2000 randomizations of sapling and seed locations (see Materials and methods for details)

Species (no. adults)	Recruited saplings				Dispersed, intact seeds			
	No. recruits	Observed distance	Expected distance	Proportion of randomizations†	No. seeds	Observed distance	Expected distance	Proportion of randomizations†
<i>Caraipa densifolia</i> (5)	43	21.7	23.8	0.187	32	13.4	33.6	0.006*
<i>Celtis shippii</i> (14)	7	22.9	36.3	0.057	110	26.9	44.0	0.035
<i>Clarisia racemosa</i> (8)	5	29.1	26.0	0.690	288	27.3	30.4	0.203
<i>Drypetes amazonica</i> (10)	11	24.2	26.6	0.248	35	21.0	25.3	0.267
<i>Leonia glycyarpa</i> (9)	19	22.5	22.6	0.488	34	22.5	25.8	0.289
<i>Mabea maynensis</i> (6)	8	12.1	37.9	0.002**	94	10.0	36.0	0.000***
<i>Matisia cordata</i> (9)	9	50.0	50.7	0.403	109	40.8	44.1	0.402
<i>Otoba parvifolia</i> (23)	24	35.6	29.7	0.978*	85	15.6	25.4	0.143
<i>Oxandra acuminata</i> (10)	60	19.2	25.5	0.000***	279	37.9	39.4	0.314
<i>Oxandra espinata</i> (10)	7	19.2	18.7	0.575	192	18.4	23.2	0.076
<i>Pseudolmedia laevis</i> (5)	21	16.2	15.3	0.740	485	22.5	21.6	0.636
<i>Quararibea wittii</i> (66)	67	15.0	14.0	0.873	82	13.2	12.4	0.716
<i>Ruizodendron ovale</i> (12)	8	53.4	34.9	1.000***	57	43.3	33.7	0.961
<i>Theobroma cacao</i> (16)	17	34.0	25.8	0.974	16	23.0	28.1	0.216
<i>Trichilia pleeana</i> (3)	20	38.3	39.6	0.360	82	29.0	41.3	0.021*
<i>Trichilia poeppigii</i> (14)	24	22.1	21.0	0.754	48	23.0	24.9	0.414
<i>Virola calophylla</i> (5)	5	61.9	51.6	0.788	127	60.5	59.6	0.552

†The proportion of randomizations in which the median distance to closest fruiting adult was less than the observed value. If the proportion is less than 0.025 or more than 0.975, then according to this 2-tailed test, saplings are significantly non-random in their distribution with respect to fruiting adults. The level of significance is indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

data from the 1.44-ha seed-trapping plot to estimate the size at which each species becomes reproductive, taking the point of inflection of the logistic. Any adult larger than the predicted reproductive size threshold in the broader 4-ha tree plot that was closer to some saplings than the nearest known fruiting adult within the 1.44 ha was added to the file of adults used to compute the distances. For *Trichilia pleeana*, which had only three fruiting individuals in the trapping grid, observations outside the tree plot were added to determine the reproductive size threshold. Secondly, we assessed whether species that should be particularly sensitive to boundary effects (i.e. those with a low number of fruiting individuals in the trapping grid) significantly biased our results. Specifically, we used regression to determine whether the difference between the observed and expected distance to conspecific fruiting adults varied with the number of adults in the trapping grid. There was no significant relationship for saplings ($R^2 = 0.001$, $P = 0.87$) or seeds ($R^2 = 0.02$, $P = 0.29$). This suggests that any remaining cryptic boundary effect in the data was minimal and could be ignored.

WINNING BY FORFEIT

We operationally defined ‘winning by forfeit’ as [1 – the proportion of traps that failed to capture seeds] in a given year. As a matter of relevance, we also quantified the diversity of the 30 species of seeds used to calculate the values in Table 1 that fell into each of the 289 traps during each of the 6 years of monitoring.

Results

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In most species, reproduction was restricted to large individuals with diameters in excess of 20 or 30 cm. Once an individual

becomes reproductive, fruiting episodes are annual except in a few species that exhibit multiannual rhythms. All but three of the 30 species included in this analysis are zoochorous. Gross fecundities of the 30 species, expressed as the mean number of potentially viable seeds falling per m^2 per year, varied from 0.012 for *Agonandra brasiliensis*, a species with a 1.1-g seed (dry wt) to 56 for *Hyeronima laxiflora*, a species with a 0.01-g seed (Table 1). Net fecundities (intact seeds after cookie-cutter exclusion) were much lower, ranging from 0.012 $m^{-2} year^{-1}$ for *Agonandra* to 0.64 for *Pseudolmedia laevis*, a common primate-dispersed species with 0.1-g seeds. Note that net fecundity did not exceed 1 $m^{-2} year^{-1}$ for any species in the community except perhaps for *Ficus* spp. and possibly some other small-seeded hemiepiphytes or gap-colonizing species that are not considered in this analysis because their saplings do not regularly occur in the advance regeneration.

The proportion of gross fecundity that appeared in traps directly under the crowns of fruiting trees varied from 0.00 to 0.99 with a median value of 0.67 (Table 1). Thus, a majority of species dropped large fractions of their crops under the parent crown. At the other extreme, nearly 100% of the crops of several species, among them, *A. brasiliensis*, *Batocarpus amazonicus*, *Chrysophyllum venezuelanense*, *Nectandra longifolia* and *Sorocea pileata*, were scattered by dispersers as intact seeds.

‘Seed limitation’, defined by Clark, Macklin & Wood (1998) as the proportion of sites (here, 0.5- m^2 traps) that failed to capture seeds of a given species over the 6-year monitoring period was high, whether evaluated via gross fecundity (median = 0.80) or net fecundity (median = 0.89). ‘Source limitation’ (the proportion of sites not reached by seeds if the observed seed rain were Poisson-distributed) was considerably

lower using gross fecundity (median = 0.26) than net fecundity (median = 0.78) because undispersed propagules are strongly clumped. ‘Dispersal limitation’, defined as the proportion of traps that received seeds relative to the expected number under a Poisson dispersion, was greater using gross fecundity (median = 0.64) than net fecundity (median = 0.45) because seeds are so unevenly distributed across traps when undispersed seeds are included.

DISPERSION OF SAPLINGS AND SEEDS WITH RESPECT TO FRUITING ADULTS

The measures of dispersal limitation summarized in the previous paragraph emphasize the evenness of the seed rain, but they do not reveal how seeds are being distributed, either with respect to reproductive adults or to the recruitment of saplings. To examine these issues, we tested observations against a null hypothesis of spatial randomness. In this section, the number of species investigated was only 17 because each one had to satisfy multiple selection criteria as explained above.

Saplings of most species recruiting into the plot appeared at random locations, although saplings of a few species recruited closer to or farther from fruiting adults than expected by chance (Table 2, Fig. 1). Analyses that used all the saplings that occurred in the plot (1997–2006) yielded similar results (see Table S1 in Supporting information). Considering all 17 species together, saplings were neither closer to nor farther from fruiting adults than expected by chance (for recruits:

mean difference = 0.1 m, paired t -test: $t = 0.05$, $P = 0.963$; for all saplings: mean difference = 0.0 m, paired t -test: $t = 0.00$, $P = 0.997$).

Using the assumption of ‘all seeds are equal’ (i.e. gross fecundity), the seeds of nearly all species fell closer to fruiting adults than expected by chance (Table S1). This is particularly evident when all 17 species are considered together (mean difference = -19.7 m, paired t -test: $t = -6.21$, $P < 0.0001$). However, when the analysis was restricted to dispersed intact seeds (net fecundity); we found that seeds were distributed at random with respect to fruiting adults in all but three species (Table 2, Fig. 2). Interestingly, one of these species is explosively dispersed (*Mabea maynensis*) and another is wind dispersed (*Caraipa densifolia*); the remaining 15 species are zoochorous. Dispersed, intact seeds were slightly closer to fruiting adults than expected by chance when all 17 species were examined collectively, but much less so that when all potentially viable seeds were included in the analysis (mean difference = -6.1 m, paired t -test: $t = -3.02$, $P = 0.008$).

Comparing the median distances of dispersed intact seeds (net fecundity scenario) and saplings to the nearest reproductive conspecific, we found a strong positive relationship (Fig. 3). The slope did not differ significantly from 1.0 (t -test: $t = -0.33$, $P = 0.371$), and the intercept did not differ significantly from 0 (t -test: $t = 0.98$, $P = 0.340$). When comparing the median distance of all viable seeds (gross fecundity scenario) and saplings to the nearest reproductive conspecific, the intercept differed significantly from 1.0 ($t = 4.23$,

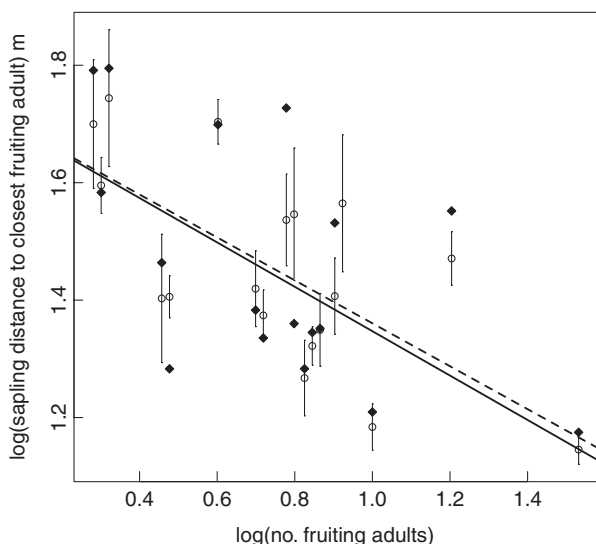


Fig. 1. The observed versus expected median distance of recruited saplings to the closest fruiting adult for 17 tree species at Cocha Cashu biological station. The logarithm (base 10) of the distances in metres is plotted against the logarithm of adult abundance. For the purpose of visualization, best-fit linear regressions for the observed (solid line) and expected (dashed line) values are shown. Solid diamonds give the observed distances. The corresponding hollow circles and error bars give the mean distance and standard deviation across 2000 randomizations for each species. The points were jittered slightly along the x -axis so that species with the same number of fruiting adults do not overlap.

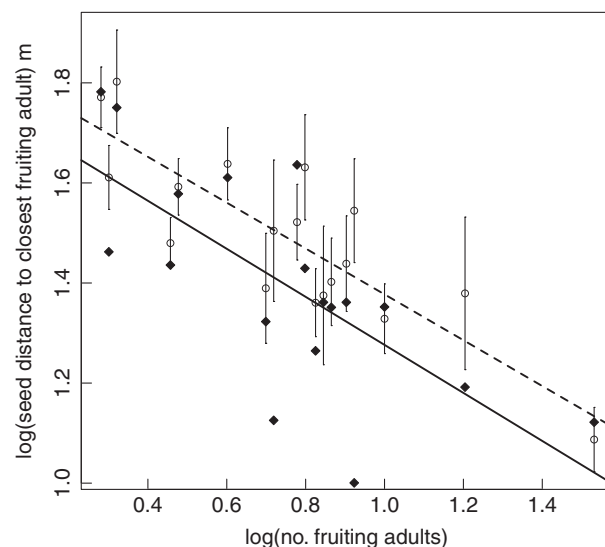


Fig. 2. The observed versus expected median distance (m) of dispersed, intact seeds to the closest fruiting adult for 17 tree species at Cocha Cashu. The logarithm (base 10) of the distances in metres is plotted against the logarithm of adult abundance. For the purpose of visualization, the best-fit linear regressions for the observed (solid line) and expected (dashed line) values are shown. Solid diamonds give the observed distances. The corresponding hollow circles and error bars give the mean distance and standard deviation across 2000 randomizations for each species. The points were jittered slightly along the x -axis so that species with the same number of fruiting adults do not overlap.

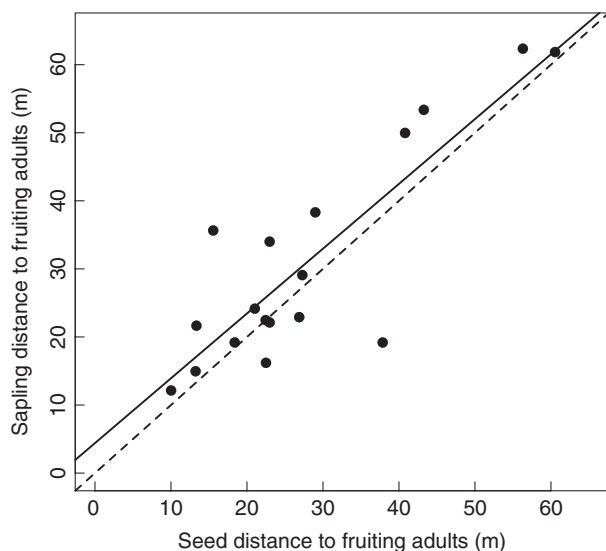


Fig. 3. The median distance to closest fruiting adults of recruited saplings versus dispersed, intact seeds for 17 tree species at Cocha Cashu. The observed, best-fit linear relationship is shown (solid line) as well as the 1:1 linear relationship (dashed line).

$P < 0.001$), whilst the slope was marginally significantly different from 0 ($t = -1.51$, $P = 0.076$).

WINNER BY FORFEIT

Using 30 of the most common species in the seed rain, we quantified the number of equally common species of intact seeds arriving in each trap during each of the 6 years of monitoring for a total of 1730 trap-years (Fig. 4). These 30 species constitute 45% of the individual non-palm subcanopy and canopy trees in the plot. Yet, the collective seed rain of these species was remarkably scant. Not a single seed of any of the 30 species was recovered in 37% of the trap-years. The modal diversity of 1–2 equally common species was found in 41% of trap-years and higher diversities were recovered in only 22%

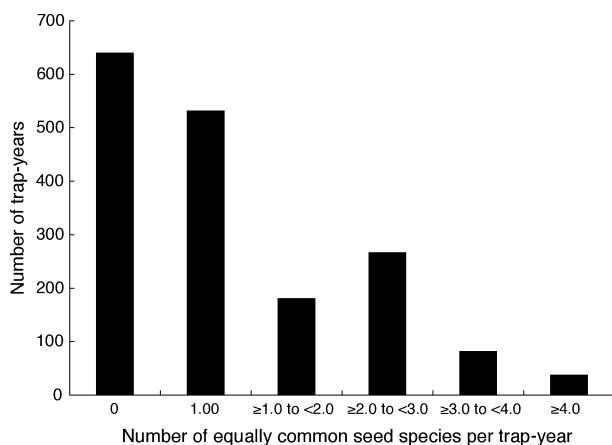


Fig. 4. Diversity (as number of equally common species) of 30 species of seeds falling into 289 0.5-m² traps over a 6-year monitoring period. $N = 1734$ trap-years.

of trap-years. Only 7% of trap-years registered even 10% of the potential diversity represented by the 30 species.

Discussion

FECUNDITY

Fecundity was low across the entire community, whether based on the ‘all seeds are equal’ model or only on dispersed ‘intact’ seeds. For dispersed intact seeds, the rain was less than 1 seed m⁻² year⁻¹ for all species. Yet, this is a highly productive floodplain site characterized by deep, fertile, neutral soils, an exceptionally large standing biomass of trees and one of the highest animal biomasses recorded in the Neotropics (Gentry 1990; DeWalt & Chave 2004; Peres 2008; Endo *et al.* 2010). Whether similar results would be obtained at other localities is work in progress.

Based on an earlier analysis of saplings under conspecific adults, it was estimated that ≥94% of saplings of the 19 most common tree species in this community and ≥98% of the saplings of 75 less common species arose from dispersed seeds (Terborgh *et al.* 2002). Now that we have an appreciation of how sparse the rain of dispersed seeds is relative to that of undispersed seeds, it is obvious that for most species, the per-capita success of dispersed seeds is many times higher than that of undispersed seeds (Terborgh *et al.* 2002; Swamy *et al.* 2010).

The low net seed rain for all species considered (< 1 seed m⁻² year⁻¹) raises serious questions about the operation of density dependence in hyperdiverse tree communities except perhaps in zones of high-density seedfall around reproductive trees (Condit, Hubbell & Foster 1994; Wills *et al.* 1997; Hubbell *et al.* 1999; Harms *et al.* 2000). Alternatively, distance-dependence, as proposed by Janzen (1970) and Connell (1971), assumes that the per-capita success of seeds increases with distance from the parent tree, a prediction that is affirmed by the closer fit of sapling recruitment to net versus gross seed fall.

Dispersed seeds appear to be scattered randomly across the forest floor except in certain ‘hot’ spots like roost trees and habitual latrines and under the same or other preferred fruiting species (Fragoso, Silvius & Correa 2003; Russo & Augspurger 2004; Terborgh & Nuñez-Ituri 2006). Whether such hotspots of seed deposition are numerically important in tree recruitment has yet to be adequately investigated.

New techniques for studying dispersal are providing insights into the distances seeds are displaced by dispersers. These include direct observations of seed-carrying dispersers (Holbrook & Smith 2000; Russo, Portnoy & Augspurger 2006) and reconstructions from parentage analysis (Hardesty, Hubbell & Bermingham 2006). Both methods concur in affirming that seeds of tropical forest trees are commonly, if not typically, transported > 100 m from source trees. Holbrook & Smith (2000) for example, document that two species of African hornbills may carry seeds as far as 3.5 and 6.9 km from source trees. Such distances represent multiples of the mean nearest-neighbour distance of adults in the population, implying that mixing of seeds from different sources is extensive. Parentage

analysis suggests that the seed parent of a given seedling is seldom the nearest adult (Hardesty, Hubbell & Bermingham 2006).

Such observations reinforce the working hypothesis of this report, namely, that nearly all saplings arise from dispersed seeds and that undispersed seeds seldom succeed. The picture that emerges when undispersed seeds are discounted contrasts strongly with the 'all seeds are equal' assumption that is usually made when modelling seed shadows (Clark *et al.* 2005; Muller-Landau *et al.* 2008). Our results suggest a well-mixed rain of dispersed seeds that is limited mainly by its scarcity.

SEED, SOURCE AND DISPERSAL LIMITATION

To better document recruitment limitation as decomposed into the constituent processes of limited fecundity and distribution, we quantified three concepts proposed by Clark, Macklin & Wood (1998) and further elaborated by Muller-Landau *et al.* (2002): seed limitation, source limitation and recruitment limitation (see materials and methods). Seed limitation was extreme, as nearly 90% of traps failed to catch intact seeds of 30 common species each year (gross 0.80, net 0.89). Source limitation was more pronounced using gross fecundity (median = 0.26) than net fecundity (median = 0.79). The large discrepancy between the two values derives from the strong skewing of seed and fruit fall under fruiting adults. Muller-Landau *et al.* (2002) found similar low values using gross fecundity. However, because undispersed seeds seldom produce saplings, we feel that net fecundity is the more biologically appropriate measure to use. Dispersal limitation, defined as the proportion of traps that received seeds relative to the expected number under Poisson dispersion, was greater using gross fecundity (median = 0.64) than net fecundity (median = 0.45) because seeds are so unevenly distributed across traps when undispersed seeds are included.

DISPERSION OF SAPLINGS AND INTACT SEEDS WITH RESPECT TO FRUITING CONSPECIFICS

The definitions of seed and dispersal limitation considered in the paragraph above do not take into account the spatial characteristics of the seed rain relative to reproductive adults. Using a randomization procedure, we calculated the expected distances to the nearest fruiting conspecific adult of small saplings and traps that caught seeds of each species if they were randomly redistributed and then compared them to observed distances. For the majority of species, we found that the distances at which dispersed seeds are falling and at which saplings are recruiting in this forest are highly concordant.

The 'all seeds are equal' approach, in which seeds contained in ripe fruits and partially processed fruits are grouped with dispersed seeds results in the highly aggregated distributions typical of computed dispersal kernels (Clark, Macklin & Wood 1998; Clark *et al.* 2005; Muller-Landau *et al.* 2008). If all such seeds truly possessed equal prospects for success, sapling recruitment would be clustered around parent trees. Instead, we find that the distribution of intact seeds very closely

matches that of concurrently recruited saplings (Fig. 3). This finding, coupled with the observed low-density seed rain, strongly suggests that there is little or no density-dependent thinning of conspecifics from the dispersed seed stage onwards.

The disparate historical origins of different components of this project resulted in non-coincident periods of monitoring of sapling recruitment (1998–2006) and seedfall (2002–2008). At present there is little information to suggest the age of saplings attaining 1 m in height (Hubbell 2004) and in any case different species are sure to vary widely in this respect. What can be stated in confidence is that most of the individual trees that produced fruit crops during the 6 years, we monitored seedfall were large members of their respective species that had been present in the plot for decades previously. We thus feel that a small disparity in the periods of sapling recruitment and seedfall would have little consequence for the data.

WINNER BY FORFEIT

The concept of 'winner by forfeit' has intuitive appeal as an explanation for spatial patterning and diversity maintenance, but to our knowledge, has not previously been examined empirically. Our results, based on 0.5-m² seed traps, unequivocally support the notion that most species fail to arrive at most sites in most years. Of the 30 species considered in the analysis, seeds of none arrived in 37% of the traps in a given year and seeds of only one arrived in another 30%. How one interprets these observations depends greatly on scale. At the scale of 0.5 m², winner by forfeit appears to be pervasive, implying a large stochastic element in recruitment, but at the scale of a hectare or square kilometre, large numbers of species have an opportunity to compete. Whereas, stochastic processes clearly operate at the scale of individual establishment events, composition at the landscape scale appears to be highly deterministic (Terborgh, Foster & Nuñez 1996; Pitman *et al.* 2001; Kobe & Vriesendorp 2009). We thus feel that the winner by forfeit has limited value as an explanation for diversity maintenance.

Conclusions

Our results affirm that seed dispersal is a critical process in tropical forests and that undispersed seeds contribute little or nothing to sapling recruitment (Howe 2000; Terborgh *et al.* 2002). The scant rain of dispersed seeds ensures that the winner by forfeit process operates pervasively at the scale of individual seeds and seedlings, but on larger scales, all species have the opportunity to compete for establishment opportunities (Clark *et al.* 2007). However, if dispersal is impeded, for example, by decimating the community of dispersers, large distortions in tree recruitment result (Stoner *et al.* 2007; Terborgh *et al.* 2008; Vanthomme, Bellé & Forget 2010). Knowing that sapling recruitment occurs almost exclusively from dispersed seeds, the fact that the rain of dispersed seeds is < 1 m⁻² year⁻¹ for all species considered effectively precludes a role for density dependence in recruitment (Wright 2002).

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Supporting Information

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

Table S1. Observed versus expected median distance to closest fruiting adult for all small saplings and all seeds.

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