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Effects of bamboo stands on seed rain and seed limitation in a rainforest

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ABSTRACT

Bamboos often negatively affect tree recruitment, survival, and growth, leading to arrested tree regeneration in forested habitats. Studies so far have focused on the effects of bamboos on the performance of seedlings and saplings, but the influence of bamboos on forest dynamics may start very early in the forest regeneration process by altering seed rain patterns. We tested the prediction that the density and composition of the seed rain are altered and seed limitation is higher in stands of *Guadua tagoara* (B or bamboo stands), a large-sized woody bamboo native from the Brazilian Atlantic Forest, compared to forest patches without bamboos (NB or non-bamboo stands). Forty 1 m^2 seed traps were set in B and NB stands, and the seed rain was monitored monthly for 1 year. The seed rain was not greatly altered by the presence of bamboos: rarefied seed species richness was higher for B stands, patterns of dominance and density of seeds were similar between stands, and differences in overall composition were slight. Seed limitation, however, was greater at B stands, likely as a resulted of reduced tree density. Despite such reduced density, the presence of trees growing amidst and over the bamboos seems to play a key role in keeping the seeds falling in B stands because they serve as food sources for frugivores or simply as perches for them. The loss of such trees may lead to enhanced seed limitation, contributing ultimately to the self-perpetuating bamboo disturbance cycle.

1. Introduction

Bamboos are known to influence forest structure and dynamics by casting a dense shade in the forest understory (Guilherme et al., 2004), providing preferred microhabitats for seed predators (Iida, 2004), and physically damaging seedlings and saplings (Griscom and Ashton, 2006). As a result, bamboos often negatively affect tree recruitment, survival, and growth, leading to arrested tree regeneration (Griscom and Ashton, 2003; Guilherme et al., 2004; Campanello et al., 2007). Such process, together with forest disturbances (either natural or anthropogenic) that permit the permanent regeneration and expansion of bamboo stands, may lead to great expanses of bamboo-dominated forests, as occur in southwestern Amazonia, where it approximately 180,000 km^2 of forest are dominated by *Guadua weberbaueri* and *G. sarcocarpa* (Nelson, 1994; Griscom and Ashton, 2003).

Although emphasis has been put on the impact of bamboos upon the growth and survival of seedlings and saplings, the influence of bamboos on forest dynamics may start very early in the forest regeneration process by altering seed rain patterns. With long, flexible and often thin culms, bamboos have an architecture that markedly differs from forest trees. Such particular architecture, together with the fact that bamboos do not produce fleshy fruits, likely make bamboo stands particularly unattractive to seed dispersers. Birds that frequently use bamboo stands are essentially insectivorous (Stotz et al., 1996).

In this paper we tested the prediction that the composition of the seed rain is altered, its density is reduced, and seed limitation is higher in forest patches dominated by bamboos when compared to patches without bamboos. Seed limitation is defined as the inability of seeds to reach all potential recruitment sites, either due to lack of dispersal or to low seed production, and has profound implications for population and community dynamics and species diversity (Tilman, 1994; Hurtt and Pacala, 1995).

We monitored seed rain falling in a mosaic formed by old-growth forest interspersed by patches of the bamboo *Guadua tagoara* (Nees) Kunth, a large-sized, semi-scandent woody bamboo native from the Brazilian Atlantic Forest. The culms (with total length reaching up to 20 m, and 10 cm diameter; Alves, 2007) are erect in the base and scandent towards the apices, growing over and amidst the adjacent vegetation with the aid of recurved thorns serving as grappling hooks. It is a monocarpic species with a life

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cycle lasting on average 7.4 years (Alves, 2007). *G. tagoara* is considered an aggressive species in secondary forests, where negatively impacts tree regeneration (Rother, 2006; Fantini and Guries, 2007). Possibly facilitated by anthropogenic (e.g., logging, palm [*Euterpe edulis*] heart extraction), and natural disturbances (e.g., landslides, treefall gaps), the species dominates wide areas of the Atlantic Forest in SE Brazil (*ca.* 15,000 ha in the region of this study; Alves, 2007), being considered a management problem inside forest reserves (Araujo, 2008).

2. Methods

2.1. Study area

The study was conducted in a 10-ha permanent plot set at the Carlos Botelho state park, a reserve with over 37,000 ha of well-preserved Atlantic rain Forest (*sensu* Morellato and Haddad, 2000) located in the state of São Paulo, SE Brazil. The park forms with other adjacent reserves a continuous block of over 120 thousand ha, one of the largest in the whole Atlantic Forest. The study site (24°10′S, 47°56′W; 350–450 m a.s.l.) is covered by tall (20–30 m) lowland old-growth forest with an opened understory where the palms *E. edulis* (269.8 individuals ha^{-1}; unpublished data) and *Geonoma* spp., and arborescent ferns (Cyateaceae) are common. Every tree >15 cm pbh (perimeter at breast height; corresponding to 4.8 cm dbh) within the 10-ha plot was initially tagged and identified to species level. Myrtaceae, Lauraceae, Rubiaceae, Fabaceae and Sapotaceae are the richest plant families (Dias, 2005). During the study period, the mean temperature was 21.1 °C (range 17.4–25.2 °C), and the site received 3384 mm of rainfall. Rains are well distributed throughout the year, but a rainiest and hottest season occurs from December to March.

Approximately 3 ha of the plot are covered by *G. tagoara* stands forming clumps throughout the plot. Within such clumps, trees of different species often appear with their crowns above the bamboo foliage.

2.2. Seed rain

Seed rain was sampled from June 2004 to June 2005 in 1 m^2 seed traps composed of wooden boxes lined with a fine plastic net (1 mm mesh) and suspended 10 cm above the ground. Eighty traps were haphazardly set in stands with and without bamboos (referred to as B for "bamboo stands", and NB for "no bamboo stands", respectively). B and NB stands received 40 traps each at least 20 m apart from each other. Traps were emptied once a month and the material collected was brought to the lab where seeds were counted and identified to the lowest taxonomic level possible by comparison with a reference collection assembled during the study, and also by consulting the literature and specialists. In addition, based on the previous experience of the authors, and the seed morphology, seeds were classified according to the dispersal syndrome (anemochorous, zoochorous, and autochorous; *sensu* Van der Pijl, 1982) and plant habit (tree, shrub, herb, liana, epiphyte – including hemi-epiphytes). Plant classification follows APG II (2003).

To relate the seed rain to the composition of the vegetation surrounding each seed trap we got from the 10-ha permanent plot database the number of individuals and tree species (>15 cm pbh) present in a 10-m radius circular area (314.1 m^2) centered at each trap.

2.3. Data analyses

To graphically compare the seed rain profile between stands, we constructed separate relative abundance curves for B and NB. The abundance of each seed species was log-transformed and plotted in a bi-dimensional plane from the most to the least abundant (Magurran, 1988).

An analysis of similarity (ANOSIM) was performed to compare the similarity in the composition of the seed rain sampled at B and NB. ANOSIM is a non-parametric permutation procedure that uses a test statistic (R) to compare the level of similarity between and within groups (B and NB stands in our case; Clarke, 1993; Clarke and Warwick, 1998). R ranges from -1 to +1. Differences between stands would be suggested by R values greater than zero, indicating that the seed rain composition was more dissimilar between than within groups. ANOSIM was performed upon a matrix of seed abundance among seed traps across seed species. We used Bray–Curtis distances as a measure of dissimilarity among seed traps. The significance of R was determined by comparison with the values obtained by 10,000 randomizations implemented in the software PAST (version 1.81; Hammer et al., 2001).

Temporal and spatial (i.e., between NB and B stands) variation in seed density was tested with repeated measures ANOVA. Differences in the proportion of dispersal syndromes and plant habits between stands were assessed with chi-square tests. Rarefaction analyses were used to compare the seed species richness sampled at B and NB, and also to compare the abundance of trees surrounding seed traps at these stands. Comparisons were based on confidence intervals derived from 1000 iteractions implemented in EcoSim 7.0 (Gotelli and Entsminger, 2001). For rarefaction analyses we report average rarefied values plus variance (σ), and 95% confidence intervals (CI).

The abundance of trees in the 10-m radius around seed traps was compared between B and NB with a t-test applied to square-root transformed data. To evaluate whether stands differ in the frequency of long-distance dispersal events, the seed species sampled at each trap was divided as those having at least an adult within the 10-m radius or not. The former were tallied as long-distance dispersed. Although seeds having an adult nearby could also represent long-distance dispersal, with the available data we cannot sort out those originated from the near adult or from adults outside the 10-m radius. Therefore, our figures for long-distance dispersal are probably underestimated, but adequate for the purpose of comparing stands. We checked if B and NB differ in the proportion of long-distance dispersal with a t-test applied to arc-sine transformed data. The analysis was restricted only to zoochorous seeds that could be identified to species level and appeared in at least three traps.

We calculated seed limitation as the proportion of seed traps not receiving seeds after the 13 months of seed collection ("Fundamental seed limitation" sensu Muller-Landau et al., 2002). Thus, seed limitation can be expressed as

$$\text{seed limitation} = 1 - \frac{a}{n}$$

where a is the number of seed traps reached by any seed of a given species, and n is the total number of seed traps.

Seed limitation arises from limited number of seeds (source limitation) and/or limited dispersal of available seeds (dispersal limitation; Muller-Landau et al., 2002). To calculate source limitation, we followed the procedure outlined by Clark et al. (1998) by considering how many seed traps would be reached if seeds were distributed uniformly with an expectation of s/n seeds per seed trap, where s is the total number of seeds of a given species collected during the study. Defining uniform distribution stochastically as a Poisson seed rain with equal expectation everywhere (i.e. a random distribution), the proportion of seed traps at which no seed arrives under such a distribution is simply the Poisson probability of zero events given the expectation of s/n events, or

$$\text{source limitation} = \exp\left(-\frac{s}{n}\right)$$

By comparing the proportion of seed traps actually reached by seeds with the proportion of seed traps that would be reached if dispersal was uniform, we calculated limitation due to failure of dispersal as

$$\text{dispersal limitation} = 1 - \left\{\frac{a/n}{1 - \text{source limitation}}\right\}$$

Analyses involving seed limitation and its components were restricted to the 26 most abundant species sampled that could also be identified to species level, together responsible for 85.9% of total seed rain. All but *Simira corumbensis* (wind-dispersed) were zoochorous (mainly bird-dispersed), and most (88.5%) were trees (Table 1). Therefore, our figures for seed limitation did not represent the whole community but a subset of it. Differences between B and NB in the limitation indexes were accessed with Wilcoxon-paired tests. All tests were performed in STATISTICA 6.0 (Statisoft, 1999) unless otherwise noted.

3. Results

3.1. Seed rain

A total of 16,860 seeds were collected, resulting in a final density of 210.7 seeds m^{-2} (or 16.5 seeds m^{-2} $month^{-1}$). Thirty-seven plant families and 145 species or morphospecies were represented among the seeds collected. Forty-four species were identified to species level, 18 to genera, 24 to family, and 59 remained undetermined (Appendix A). The most abundant species were *Cecropia glaziovi* (Urticaceae), followed by *Hyeronima alchorneoides* (Euphorbiaceae), and *E. edulis* (Arecaceae), together responsible for 73.0% of total seed rain. The relative abundance curves for B and NB followed a log-series model (sensu Fisher et al., 1943; Fig. 1). In other words, the seed rain was dominated by a few species, whereas the majority of species occurred in low abundances. B and NB shared seven out of the ten most abundant species. Although the composition of the seed rain differed between stands the difference was slight, as denoted by the low

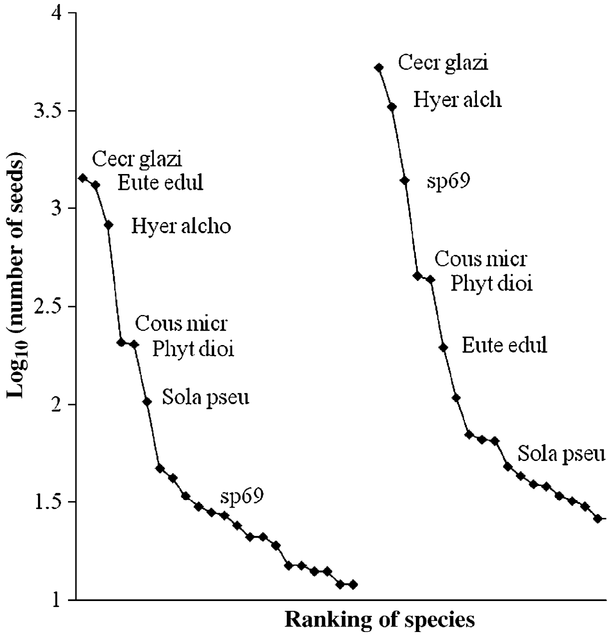

Fig. 1. Relative abundance curves for seed species collected at bamboo (B, left curve), and non-bamboo (NB) stands. In the horizontal axis, species are ranked from the most to the least abundant. Codes for the most abundant species: Cecr glaz (*Cecropia glaziovi*), Eute edul (*Euterpe edulis*), Hyer alch (*Hyeronima alchorneoides*), Cous micr (*Coussapoua microcarpa*), Sola pseu (*Solanum pseudoquina*), Phyt dioi (*Phytolacca dioica*) and sp. 69 (unidentified #69).

Table 1
Seed, source and dispersal limitation indexes (see text for definitions) for seed species at bamboo (B) and non-bamboo (NB) stands. Indexes >0.60 suggesting strong limitations are highlighted.

Species	B stands			NB stands		
	Seed limitation	Source limitation	Dispersal limitation	Seed limitation	Source limitation	Dispersal limitation
Alchornea glandulosa	**0.90**	0.35	**0.85**	**0.98**	**0.98**	<0.01
Ardisia martiana	**0.90**	**0.74**	**0.61**	**0.80**	**0.78**	0.10
Capsicodendron dinisii	**0.85**	**0.70**	0.49	**0.93**	**0.90**	0.21
Cecropia glaziovi	0.08	<0.01	0.07	0.05	<0.01	0.05
Chrysophillum viride	**0.90**	0.59	**0.76**	**0.83**	0.58	0.59
Cissampelos andromorpha	**0.95**	**0.88**	0.57	**0.95**	0.43	**0.91**
Costus spiralis	**0.95**	0.59	**0.88**	**0.98**	**0.90**	**0.74**
Coussapoua microcarpa	0.40	<0.01	0.40	0.25	<0.01	0.25
Cryptocarya moschata	**0.93**	**0.86**	0.46	**0.95**	**0.93**	0.31
Eugenia mosenii	**0.98**	**0.98**	<0.01	**0.90**	**0.67**	**0.70**
Euterpe edulis	0.15	<0.01	0.15	0.15	0.01	0.14
Hyeronima alchorneoides	0.20	<0.01	0.20	0.08	<0.01	0.08
Meliosma sellowii	**0.98**	**0.98**	<0.01	**0.88**	**0.78**	0.43
Monstera adansoni	**0.85**	**0.82**	0.17	0.58	0.19	0.47
Neomitrantes glomerata	**1.00**	**1.00**	**1.00**	**0.75**	0.52	0.48
Noratea brasiliensis	**1.00**	**1.00**	**1.00**	**0.98**	0.17	**0.97**
Phytolacca dioica	0.58	0.01	0.57	0.28	<0.01	0.27
Psychotria pubigera	**0.75**	0.51	0.49	**0.73**	0.54	0.41
Myrsine hermogenesi	**0.75**	**0.76**	<0.01	**0.73**	0.58	0.35
Rollinea sericea	**0.85**	**0.69**	0.52	**0.93**	0.39	**0.88**
Rudgea recurva	**0.95**	**0.90**	0.47	**0.95**	**0.70**	**0.83**
Sapium glandulatum	**1.00**	**1.00**	**1.00**	**0.90**	0.07	**0.89**
Simira corumbensis	**1.00**	**1.00**	**1.00**	**0.93**	0.52	**0.84**
Solanum pseudoquina	**0.75**	0.08	**0.73**	0.53	0.30	0.32
Tetrastylidium grandifolium	**0.95**	**0.95**	<0.01	**0.83**	**0.74**	0.32
Virola bicuhyba	**0.83**	**0.70**	0.41	**0.93**	**0.70**	**0.75**

R value (ANOSIM: $R = 0.06$, $p = 0.001$). Most of the seeds that could be assigned to a plant habit came from trees (96.0%, $n = 14{,}384$ seeds), with no difference between stands in the proportion of trees and other plant habits among the seeds collected ($\chi^2 = 0.01$, d.f. = 1, $p = 0.91$). Similarly, the vast majority of seeds was zoochorous (98.5%, $n = 15{,}027$ seeds), and B and NB stands did not differ in the proportion of zoochorous and non-zoochorous seed species ($\chi^2 = 0.02$, d.f. = 1, $p = 0.88$).

NB received a greater number of seeds (12,155 seeds or 151.9 seeds m^{-2}) than B (4705 seeds or 58.8 seeds m^{-2}), mainly due to the contribution of *C. glaziovi*, *H. alchorneoides*, and an undetermined seed species (Appendix A). Seed rain density did not differ between stands ($F_{1,78} = 3.41$, $p = 0.14$), but varied temporally, with a peak in April 2005 for both stands ($F_{12,936} = 12.78$, $p < 0.001$). A marginally significant interaction occurred between stand type and time ($F_{12,936} = 1.63$, $p = 0.08$). Although a greater number of seed species or morphospecies were collected in NB (117) than in B (100) stands, rarefaction analysis revealed that after accounting for the greater abundance of seeds at NB, these stands presented a smaller seed species richness than B stands (average rarefied richness for NB: 85.8 species, $\sigma = 14.3$, 95% CI: 79–93 species).

The density of trees around seed traps was greater in NB than in B (1278.8 ± 431.7 trees ha^{-1} vs. 1007.5 ± 551.8 trees ha^{-1}, respectively; $t = 2.89$, d.f. = 78, $p = 0.005$). *E. edulis* was the most common tree species, with similar densities in both stands (202.1 ± 100.6 trees ha^{-1} vs. 210.9 ± 118.8 in B and NB, respectively; $t = 0.56$, d.f. = 78, $p = 0.57$). Although a greater number of species occurred in NB (153) than at B (140), rarefaction analysis showed no difference in species richness between stands (average rarefied richness for B stands: 145.1 species, $\sigma = 6.2$ species, 95% CI: 140–150 species).

Comparing the seed rain sampled at each seed trap with the surrounding vegetation revealed that the proportion of long-distance (>10 m) dispersal did not differ between B (0.67 ± 0.34, $n = 20$) and NB (0.74 ± 0.29, $n = 14$) stands ($t = 0.45$, d.f. = 32, $p = 0.65$).

3.2. Seed limitation

Seed limitation varied substantially among species, from almost nonexistent (e.g., *C. glaziovi*) to very strong (>0.90; Table 1), but it was high for most species: for 21 and 19 of the 26 seed species >70% of seed traps failed to receive any seed at B and NB, respectively. B stands, however, had a higher seed limitation than NB ($Z = 2.54$, $p = 0.01$, $n = 26$ pairs; Fig. 2). Source limitation differed marginally between B and NB ($Z = 1.83$, $p = 0.08$, $n = 26$ pairs; Fig. 2), while dispersal limitation did not differ at all ($Z = 0.25$, $p = 0.80$, $n = 26$ pairs; Fig. 2).

A within stand comparison of the predominance of source or dispersal limitation revealed that none predominate either at B (for 11 species source limitation was higher than dispersal limitation, whereas for 15 species the reverse was true; $\chi^2 = 0.09$, d.f. = 1, $p = 0.76$) or at NB stands (13 and 9 species, respectively; $\chi^2 = 0.08$, d.f. = 1, $p = 0.78$), indicating that both the number of seeds and dispersal of available seeds are important contributors to seed limitation depending on species. In an inter-stand comparison, 15 out of 22 species whose seeds were collected in both stands were consistent regarding the predominance of either source or dispersal limitation, what again suggests a species-specific nature of limitation processes acting upon species.

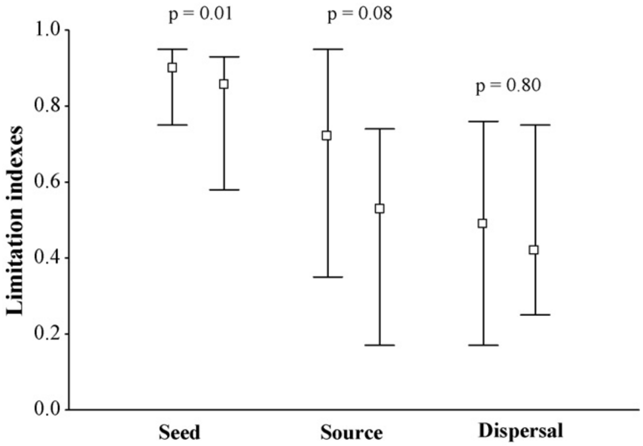

Fig. 2. Seed, source and dispersal limitations for 26 plant species sampled in bamboo (left lines) and non-bamboo (right lines) stands. Median (squares), and 25–75% percentiles (vertical lines) are represented. *P* values are based on Wilcoxon-paired tests. Limitation indexes (depicted in the *Y*-axis) were calculated for each of these kinds of limitations as defined in the text.

4. Discussion

The seed rain sampled at B and NB stands did not differ in the extent and direction we initially predicted. Rarefied seed species richness was higher for B stands, patterns of dominance and density of seeds were similar between stands, and differences in overall composition were slight. Such results might have arisen from the spatial distribution of B stands, immersed in a matrix of old-growth forest, thus with an abundance of seed sources and seed dispersers nearby. However, this not suffice to explain the similarities if seed dispersers completely avoided B stands. Given that most of the seeds sampled were zoochorous (especially bird-dispersed) and the frequency of long-distance dispersal did not differ between B and NB stands, we conclude that frugivorous animals visited B stands frequently. For this, the presence of trees growing in bamboo stands seems to be important. Although less dense than in NB stands, the density of trees in B stands was considerable, averaging over 1000 trees/ha. These trees, either witnesses of the forest prior to the expansion of the bamboo or that managed to grow amidst the bamboo, promote the arrival of seeds in bamboo-dominated forest patches by acting as food sources for frugivores or simply as perches for them. As Willson and Crome (1989) noted, the existence of perches could have marked effects on the seed rain in disturbed areas.

Of particular interest for forest dynamics was the high abundance of seeds of *C. glaziovi*, a typical pioneer species with dormant seeds in the soil, despite the relatively low abundance of adults in the area (11 and 7 *C. glaziovi* adults surveyed in B and SB stands, respectively). This apparent incongruence only reflects the well-known high efficiency seed dispersal system of *Cecropia* species, characterized by high fecundity and a variety of seed dispersers that includes birds, bats, and marsupials (Fleming and Williams, 1990). Dropping a great amount of seeds in bamboo stands, *C. glaziovi* and other pioneer plant species may benefit from the monocarpic life cycle of *G. tagoara* to rapidly occupy the gaps left behind by dying bamboo culms before they were dominate again by the next bamboo generation. Opportunities for plants to takeover patches previously dominated by *G. tagoara* after the bamboo death occurs more frequently in small and isolated bamboo stands or in the case of low fruit set after the bamboo flowering episode (Alves, 2007).

Also among the most common seeds sampled, the response of *E. edulis* to the spreading of bamboos is of special interest because of its ecological importance as the dominant tree species in well-preserved Atlantic Forest areas, and also because its important socio-economic value (Reis et al., 2000). *E. edulis*, however, presents an intriguing question: how to explain the much higher density of *E. edulis* seeds in B than in NB stands given similar densities of adults in both stands? We are left with a couple of non-exclusive possibilities: first, *E. edulis* adults were more exposed to light in B than in NB stands, which may lead to the production of greater fruit crops. Second, exposed palms may be more conspicuous and attract frugivorous birds more frequently. Both these possibilities are corroborated by the unpublished data of Marina C. Côrtes, who found the number of *E. edulis* infructescences and fruits covarying negatively with canopy closure, which was in turn negatively correlated with the number of fruits ingested by individual birds. To eat more fruits a bird has to stay longer on the plant, which increases the chance of dropping the ingested seeds beneath it (Wheelwright, 1991). Whatever the mechanisms involved, the high deposition of *E. edulis* seeds may guarantee its permanence in bamboo stands because *G. tagoara* seems not to be especially detrimental to *E. edulis* populations (Fantini and Guries, 2007).

Despite the similarities in seed rain density and composition, seed limitation was higher in B stands, meaning that on average seed species failed to reach a greater proportion of seed traps in B than in NB stands. Indeed, contrary to NB, some seed species were never collected from B stands. This probably arose from the smaller absolute number of seeds that reached B stands (source limitation) rather than to the unevenness of seed distribution (dispersal limitation). Source limitation is influenced by the fecundity and density of seed-producing plants (Clark et al., 1998). We did not evaluate the differences in source fecundities between stands, but the more open conditions of B stands suggests that individual fecundities may be higher there due to increased light availability, especially for understory plants (Chazdon, 1986; Levey, 1990). The density of trees did differ between stands, being smaller at B stands. Therefore, reduced tree density is a likely determinant of the greater source limitation in B stands.

In conclusion, the seed rain is not greatly altered by the presence of bamboos. The presence of trees growing amidst and over the bamboos seems to play a key role in keeping the seeds falling in bamboo stands; either by dropping their own seeds or by promoting the activity of seed dispersers. If the density of such trees decreases with time as a consequence of the perpetuation of the bamboo dominance and suppression of tree recruitment (Griscom and Ashton, 2003, 2006), seed limitation within B stands tends to enhance. Because enhanced seed limitation potentially reduces the chance of occupation of B stands after the dye-off of bamboos, this may constitute an additional mechanism to contribute to the self-perpetuating bamboo disturbance cycle. Therefore, keeping trees growing above the bamboo layer is a management option to give the forest a chance to take over the bamboo-dominated stands.

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Appendix A. Family, species, seed abundance, dispersal syndrome and plant habit for seeds collected at bamboo (B) and non-bamboo (NB) stands

Family	Species	Seed abundance				
		Total	B	NB	Dispersal syndrome[a]	Plant habit[b]
Anacardiaceae	Anacardiaceae 1	11	1	10	Z	ST
	Anacardiaceae 2	11	2	9	Z	ST
Annonaceae	*Rollinia sericea* R.E. Fri.	53	15	38	Z	T
Apocynaceae	*Condylocarpon* sp.	6	0	6	Z	L
Araceae	*Monstera adansonii* Schott	74	8	66	Z	E
	Philodendron sp.	38	19	19	Z	E
Araliaceae	*Dendropanax cuneatum* (DC.) Decne. & Planch.	5	2	3	Z	T
Arecaceae	*Euterpe edulis* Mart.	1511	1316	195	Z	T
	Geonoma sp. 1	3	0	3	Z	S
	Geonoma sp. 2	40	8	32	Z	S
	Geonoma sp. 3	1	0	1	Z	S
Asteraceae	Asteraceae 1	1	1	0	A	HSS
	Asteraceae 2	16	7	9	A	HSS
Bignoniaceae	*Adenocalymma* sp.	1	1	0	A	L
	Bignoniaceae 1	19	4	15	A	L
Boraginaceae	*Cordia silvestris* Fresen.	6	0	6	Z	T
Burseraceae	*Protium widgrenii* Engl.	5	1	4	Z	T
Canellaceae	*Capsicodendron dinisi* (Schw.) Occhioni	18	14	4	Z	T
Celastraceae	*Maytenus* sp.	29	12	17	Z	T
Chrysobalanaceae	*Parinari excelsa* Sabine	2	1	1	Z	T
Clusiaceae	*Garcinia gardneriana* Planch. & Triana	10	6	4	Z	T
Costaceae	*Costus spiralis*	25	21	4	Z	S
Curcubitaceae	Curcubitaceae 1	11	11	0	Z	L
Elaeocarpaceae	*Sloanea* sp.	40	1	39	Z	T
Euphorbiaceae	*Alchornea glandulosa* Poepp. & Engl.	43	42	1	Z	ST
	Alchornea sp.	3	1	2	Z	T
	Hyeronima alchorneoides Allemão	4128	825	3303	Z	T
	Sapium glandulatum (Vell.) Pax	108	0	108	U	ST
Leguminosae (Fabaceae)	*Hymaenea courbaril* L.	1	1	0	Z	T
Lauraceae	*Cryptocarya moschata* Ness & Mart. ex Ness	9	6	3	Z	T
	Lauraceae 1	1	0	1	Z	T
	Lauraceae 2	1	0	1	Z	T
Malpighiaceae	*Tetrapterys* sp.	2	2	0	A	T
Marcgraviaceae	*Norantea brasiliensis* Choisy	70	0	70	Z	E
Menispermaceae	*Abuta selloana* (Miers ex Benth.) Eichler.	2	2	0	Z	L
	Cissampelos andromorpha DC.	39	5	34	Z	L

Appendix A (*Continued*)

Family	Species	Seed abundance				
		Total	B	NB	Dispersal syndrome[a]	Plant habit[b]
	Hyperbaena sp.	1	0	1	Z	L
Myristicaceae	*Virola bicuhyba* (Schott.) A. C. Smith	28	14	14	Z	T
Myrsinaceae	*Ardisia martiana* Miq.	22	12	10	Z	T
	Myrsinaceae 1	3	3	0	Z	T
	Myrsine hermogenesii Jung-Mend. & Bernacci	33	11	22	Z	T
Myrtaceae	*Eugenia cambucarana* Kiaersk.	2	1	1	Z	T
	Eugenia mosenii (Kausel) Sobral	17	1	16	Z	T
	Neomitrantes glomerata (D. Legrand) D. Legrand	26	0	26	Z	T
	Plinia complanata M. L. Kavasaki & B. Holst	2	1	1	Z	T
	Myrtaceae 1	16	5	11	Z	T
	Myrtaceae 2	2	2	0	Z	T
	Myrtaceae 3	6	4	2	Z	T
	Myrtaceae 4	52	47	5	Z	T
	Myrtaceae 5	1	1	0	Z	T
	Myrtaceae 6	4	3	1	Z	T
	Myrtaceae 7	1	0	1	Z	T
	Myrtaceae 8	1	0	1	Z	T
	Myrtaceae 9	5	0	5	Z	T
	Myrtaceae 10	15	2	13	Z	T
	Myrtaceae 11	1	0	1	Z	T
	Myrtaceae 12	1	0	1	Z	T
	Myrtaceae 13	2	0	2	Z	T
	Myrtaceae 14	8	4	4	Z	T
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	2	1	1	Z	T
Olacaceae	*Tetrastylidium grandifolium* (Baill.) Sleumer	14	2	12	Z	T
Phytolaccaceae	*Phytolacca dioica* L.	636	202	434	Z	T
Quiinaceae	*Quiina glaziovii* Engl.	9	0	9	Z	T
Rubiaceae	*Chomelia catharinae* (L. B. Sm. & Downs) Steyerm.	6	0	6	A	T
	Ixora heterodoxa Müll. Arg.	6	3	3	Z	T
	Ixora sp.	6	2	4	Z	T
	Posoqueria acutifolia Mart.	2	0	2	Z	T
	Psychotria mapourioides DC.	10	6	4	Z	T
	Psychotria pubigera Schltdl.	52	27	25	Z	ST
	Psychotria sp. 1	1	1	0	Z	ST
	Psychotria sp. 2	1	0	1	Z	ST
	Psychotria sp. 3	3	1	2	Z	ST
	Psychotria suterella Müll. Arg.	10	0	10	Z	T
	Psychotria umbellata Vell.	18	1	17	Z	ST
	Rubiaceae 1	1	0	1	Z	ST
	Rubiaceae 2	1	1	0	Z	ST
	Rudgea recurva Muell. Arg.	18	4	14	Z	T
	Simira corumbensis Standl.	26	0	26	A	T
Sabiaceae	*Meliosma sellowii* Urb.	11	1	10	Z	T
Salicaceae	*Casearia* sp.	24	24	0	Z	T
Sapindaceae	*Paullinia* sp.	8	0	8	Z	L
Sapotaceae	*Chrysophyllum innornatum* Mart.	9	0	9	Z	T
	Chrysophyllum viride Mart. & Eichl.	43	21	22	Z	T
Solanaceae	*Solanum pseudoquina* A. St.-Hil.	151	103	48	Z	T
Urticaceae	*Cecropia glaziovi* Snethlage	6671	1431	5240	Z	T
	Coussapoua microcarpa (Schott) Rizzini	660	207	453	Z	T
Undetermined	Undetermined 1	1	1	0	–	–
	Undetermined 2	1	1	0	Z	–
	Undetermined 3	1	0	1	Z	–
	Undetermined 4	31	30	1	U	–
	Undetermined 5	12	0	12	–	–
	Undetermined 6	7	0	7	–	–
	Undetermined 7	1	1	0	Z	–
	Undetermined 8	2	1	1	Z	–
	Undetermined 9	2	1	1	Z	–
	Undetermined 10	50	34	16	Z	–
	Undetermined 11	3	1	2	Z	–
	Undetermined 12	1	0	1	–	–
	Undetermined 13	15	12	3	Z	–
	Undetermined 14	12	1	11	–	–
	Undetermined 15	1	0	1	–	–
	Undetermined 16	1	1	0	–	–
	Undetermined 17	1	0	1	Z	–
	Undetermined 18	2	1	1	Z	–
	Undetermined 19	5	5	0	–	–
	Undetermined 20	2	2	0	–	–
	Undetermined 21	1	1	0	–	–
	Undetermined 22	1	0	1	Z	–
	Undetermined 23	13	11	2	Z	–
	Undetermined 24	3	2	1	Z	–

Appendix A (*Continued*)

Family	Species	Seed abundance				
		Total	B	NB	Dispersal syndrome[a]	Plant habit[b]
	Undetermined 25	1	1	0	–	–
	Undetermined 26	3	3	0	–	–
	Undetermined 27	6	6	0	–	–
	Undetermined 28	1	0	1	Z	–
	Undetermined 29	2	1	1	Z	–
	Undetermined 30	1	0	1	Z	–
	Undetermined 31	2	0	2	–	–
	Undetermined 32	18	10	8	–	–
	Undetermined 33	1	1	0	–	–
	Undetermined 34	3	1	2	Z	–
	Undetermined 35	2	0	2	–	–
	Undetermined 36	1	0	1	Z	–
	Undetermined 37	12	5	7	Z	–
	Undetermined 38	1	1	0	Z	–
	Undetermined 39	1	1	0	Z	–
	Undetermined 40	40	10	30	–	–
	Undetermined 41	1	0	1	Z	–
	Undetermined 42	1	0	1	–	–
	Undetermined 43	1421	28	1393	–	–
	Undetermined 44	1	0	1	Z	–
	Undetermined 45	1	1	0	Z	–
	Undetermined 46	1	1	0	–	–
	Undetermined 47	9	6	3	–	–
	Undetermined 48	1	1	0	Z	–
	Undetermined 49	1	0	1	Z	–
	Undetermined 50	24	12	12	Z	–
	Undetermined 51	11	8	3	U	–
	Undetermined 52	1	0	1	–	–
	Undetermined 53	66	1	65	Z	–
	Undetermined 54	1	0	1	–	–
	Undetermined 55	1	0	1	U	–
	Undetermined 56	58	15	43	–	–
	Undetermined 57	1	0	1	A	–
	Undetermined 58	2	1	1	–	–
	Undetermined 59	3	1	2	Z	–
Total		16860	4705	12155		

[a] A, anemochorous; U, autochorous; Z, zoochorous; (–) unclassified.

[b] T, tree; S, shrub; H, herb; L, liana; E, epiphyte; HSS, herb-sub shrub; ST, shrub-tree; (–) unclassified.

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