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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