Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

Research article

Demographic bottlenecks in tropical plant regeneration: A comparative analysis of causal influences

Débora Cristina Rother [a], Pedro Jordano [b], Ricardo Ribeiro Rodrigues [c], Marco Aurélio Pizo [d,*]

[a] Programa de Pós-graduação em Biologia Vegetal, Universidade Estadual Paulista, Avenida 24A, 1515, CEP 13506-900, Rio Claro, SP, Brazil
[b] Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Isla de La Cartuja, Avenida Americo Vespucio, S/N, E-41092 Sevilla, Spain
[c] Departamento de Ciências Biológicas, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Avenida Pádua Dias, 11, Caixa Postal 9, CEP 13418-900, Piracicaba, SP, Brazil
[d] Departamento de Zoologia, Universidade Estadual Paulista, Avenida 24A, 1515, CEP 13506-900, Rio Claro, SP, Brazil

ABSTRACT

Mortality factors that act sequentially through the demographic transitions from seed to sapling may have critical effects on recruitment success. Understanding how habitat heterogeneity influences the causal factors that limit propagule establishment in natural populations is central to assess these demographic bottlenecks and their consequences. Bamboos often influence forest structure and dynamics and are a major factor in generating landscape complexity and habitat heterogeneity in tropical forests. To understand how patch heterogeneity influences plant recruitment we studied critical establishment stages during early recruitment of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in bamboo and non-bamboo stands in the Brazilian Atlantic forest. We combined observational studies of seed rain and seedling emergence with seed addition experiments to evaluate the transition probabilities among regeneration stages within bamboo and non-bamboo stands. The relative importance of each mortality factor was evaluated by determining how the loss of propagules affected stage-specific recruitment success. Our results revealed that the seed addition treatment significantly increased seedling survivorship for all three species. *E. edulis* seedling survival probability increased in the addition treatment in the two stand types. However, for *S. guianensis* and *V. bicuhyba* this effect depended strongly on artificially protecting the seeds, as both species experienced increased seed and seedling losses due to post-dispersal seed predators and herbivores. Propagules of all three species had a greater probability of reaching subsequent recruitment stages when protected. The recruitment of large-seeded *V. bicuhyba* and *E. edulis* appears to be much more limited by post-dispersal factors than by dispersal limitation, whereas the small-seeded *S. guianensis* showed an even stronger effect of post-dispersal factors causing recruitment collapse in some situations. We demonstrated that *E. edulis*, *S. guianensis* and *V. bicuhyba* are especially susceptible to predation during early compared with later establishment stages and this early stage mortality can be more crucial than stand differences as determinants of successful regeneration. Among-species differences in the relative importance of dispersal vs. establishment limitation are mediated by variability in species responses to patch heterogeneity. Thus, bamboo effects on the early recruitment of non-bamboo species are patchy and species-specific, with successional bamboo patches exerting a far-reaching influence on the heterogeneity of plant species composition and abundance.

© 2012 Elsevier GmbH. All rights reserved.

Introduction

The regeneration process of plants involves a series of stages from seed production to recruitment of juveniles, including seed dispersal, seed germination and seedling establishment (Martínez-Ramos and Soto-Castro, 1993; Jordano and Herrera, 1995; Clark et al., 1999; Rey and Alcántara, 2000). This process concatenates the early consequences of seed dissemination with the early stages of seedling regeneration and strongly affects vegetation structure (Wang and Smith, 2002). Multiple factors influence these stages and determine the dynamics and spatial distribution of plant populations (Clark et al., 1999), yet the relative importance of the different mortality effects and their consequences remain poorly understood.

Seed dispersal is a particularly important phase because it connects the end of the adult reproductive cycle to the seedling stage

* Corresponding author. Tel.: +55 19 35264294; fax: +55 19 35264300.
E-mail address: pizo@rc.unesp.br (M.A. Pizo).

(Harper, 1977; Wang and Smith, 2002). For animal-dispersed plant species, seed dispersal bridges the consequences of animal movement patterns with their effects on plant recruitment. These effects in part depend upon the microhabitat where seeds are deposited and its influence on growth and mortality of both seeds and seedlings. Seed predation, herbivory, pathogen attack, and water stress, among many other mortality factors, can act on these stages representing bottlenecks for recruitment (Harms et al., 2000; Rey and Alcántara, 2000). The relative importance of each mortality factor can vary according to microhabitat conditions, resulting in spatial discordance in the performance of each stage of regeneration (Jordano and Herrera, 1995; Schupp, 1995; Schupp et al., 2002). Either increased mortalities at a given stage or marked uncoupling among the recruitment probabilities of successive stages can lead to regeneration bottlenecks, i.e., demographic transitions where the survival prospects for propagules are zero or close to zero. Despite recent efforts to understand how generalized these types of demographic bottlenecks are (García et al., 2005; Clark et al., 2007; González-Varo et al., 2012), few comparative studies have been carried out in tropical rainforests, where recruitment limitation is pervasive (Harms et al., 2000). A persistent challenge is to understand the mechanisms operating upon seed rain and seedling recruitment patterns assessed in observational studies, for instance by combining with experimental approaches.

Ideally, such a combination of observational and experimental tests should be conducted in heterogeneous environments with a varied typology of distinct habitat patches. Bamboo-dominated stands are a particular microhabitat in forests around the world. Bamboo stands may represent preferred microhabitats for seed predators (Iida, 2004), enhance the physical damage to seedlings and saplings (Griscom and Ashton, 2006), and also alter seed limitation patterns (Rother et al., 2009). As a result, bamboos often influence forest structure and dynamics (Guilherme et al., 2004) and are a major factor in generating landscape complexity and habitat heterogeneity in tropical forests. Large tracts of bamboo-dominated forests may occur, as in southwestern Amazonia, where approximately 180,000 km^2 of forest are dominated by *Guadua weberbaueri* and *G. sarcocarpa* (Nelson, 1994; Griscom and Ashton, 2003). In the Atlantic forest of SE Brazil, the endemic bamboo *Guadua tagoara* is estimated to dominate ca. 15,000 ha, being considered a management problem inside forest reserves (Araujo, 2008).

Previous studies have examined the effects of bamboos on seed rain (Rother et al., 2009), seedling establishment, and sapling performance of non-bamboo species (Griscom and Ashton, 2006). However, it is still unknown if the conditions prevailing at bamboo stands can affect propagule losses at each demographic stage, and which are the demographic bottlenecks inherent to each population stage of non-bamboo species.

Here we compared the seed rain, abundance of early established seedlings, and seedling survival of three Atlantic forest plant species (*Euterpe edulis*, *Sloanea guianensis*, and *Virola bicuhyba*) between bamboo and non-bamboo stands. We evaluated how these three stages are connected through the recruitment cycle of the focal plant species as a series of transition probabilities which depend on mortality factors. These factors determine the overall loss of propagules by affecting the three main recruitment processes (dispersal, germination and seedling survival).

To assess limitation processes that can act as demographic bottlenecks for effective recruitment, we combined seed addition experiments (Turnbull et al., 2000; Münzbergová and Herben, 2005; Clark et al., 2007) and subsequent seedling establishment, with an observational approach based on seed traps and seedling plots that has been successfully used in previous studies (e.g., Dalling et al., 2002; Müller-Landau et al., 2002; Gómez-Aparicio

et al., 2007; Mendoza et al., 2009). Combining these two approaches is fundamental to understand recruitment limitation and to interpret seed addition experiments (Clark et al., 2007). This is a central issue when attempting to assess limiting factors of local densities, where the magnitudes of limitation at both seed and seedling stages need to be evaluated. Additionally, we might also expect that coexisting species in a forest might differ in their relative positions along a seed-to-establishment limitation gradient (Müller-Landau et al., 2002) yet these positions depend on the particular microhabitat of the forest. These aspects of patch heterogeneity and limitation magnitude remain virtually unexplored in tropical forests.

Specifically, we addressed the following questions: (1) what is the extent of dispersal limitation and recruitment mortality factors for different plant species depending on microhabitat type?, (2) are there distinct demographic stages that consistently generate bottlenecks?, and (3) do compensatory effects occur in different stand types, so that high mortality in one stage is later balanced with high survival prospects for propagules? We predicted that species recruitment would vary between microhabitats, and that it would be more evident in the seedling establishment in the bamboo stands because of the environmental conditions created by the bamboo and the physical damage caused by the fall of their culms. Here, focusing on the recruitment dynamics, we aimed to identify the most important stages and factors limiting recruitment of non-bamboo plant species at forest patches under influence of bamboos, and how they compare with non-bamboo forest patches. Bamboo stands generate a marked heterogeneity in this forest type, and we predict differential responses of plant species depending on seed size, seed rain density and responses to post-dispersal mortality factors.

Material and methods

Study area and plant species

Fieldwork was conducted in a 10.2 ha permanent plot within the Carlos Botelho State Park, a reserve with over 37,000 ha of Atlantic forest (*sensu* Morellato and Haddad, 2000) located in the state of São Paulo, southeast Brazil. The lowland study site (24°10′S, 47°56′W; 350–450 m a.s.l.) is covered by old-growth forest (20–30 m height) with an open understory where the palms *E. edulis* (270 individuals ha^{-1}; D.C. Rother, unpubl. data) and *Geonoma* spp., low trees and shrubs of the *Psychotria genus*, and arborescent ferns (Cyatheaceae) are especially common. Myrtaceae (91 species), Lauraceae (43), Rubiaceae (25), Fabaceae (13) and Sapotaceae (11) are the richest plant families overall (Dias, 2005). During the study period, the mean temperature was 21.1 °C (range 17.4–25.2 °C), and the average annual rainfall was 3384 mm. Rains are well distributed throughout the year, but the rainiest and hottest season occurs from December to March (DAEE/SP, 2009).

Approximately 3 ha of the permanent plot are covered by *G. tagoara* (Nees) Kunth, a large-sized, semi-scandent woody native bamboo. *G. tagoara* forms patches (hereafter bamboo or B stands) with different shapes and sizes, varying from 400 to 20,000 m^2. These patches are interspersed with areas lacking bamboos (hereafter non-bamboo or NB stands) forming a mosaic throughout the plot. The bamboo presence means that B stands have a greater canopy opening and thicker ground litter than NB stands, with the density of culms making it hard to walk through B stands (Lima and Gandolfi, 2009). B stands are characterized by a lower density and basal area of trees > 5 cm pbh (perimeter at breast height) (Lima et al., 2012). However, non-bamboo stands, are typically covered by dense old-growth forest with an average canopy height of 20 m (Custódio-Filho, 2002). Palms (especially *E. edulis* and *Geonoma*

spp.) and tree ferns (*Alsophila* and *Cyathea* spp.) are abundant in the wet and shady non-bamboo understory (Lima et al., 2011, 2012).

E. edulis, *S. guianensis*, and *V. bicuhyba* were the three plant species selected for this study. These species were chosen because they are all bird-dispersed, all occur naturally at B and NB stands as seeds, seedlings and adults but have contrasting seed sizes (Rother, 2006). The density of individuals > 15 cm pbh at the permanent plot were 231.1, 10.5, and 17.7 individuals ha^{-1} for *E. edulis*, *S. guianensis*, and *V. bicuhyba*, respectively (unpubl. data). A survey of the three target plant species made in 40 circular plots (10 m radius) set at each stand type revealed 254 *E. edulis*, nine *S. guianensis*, and 32 *V. bicuhyba* individuals in B stands. At NB stands, 265 *E. edulis*, seven *S. guianensis*, and 13 *V. bicuhyba* trees were recorded (all >15 cm pbh; D.C. Rother, unpubl. data).

E. edulis Martius (Arecaeae) is a dominant palm found in the understory of the Atlantic forest. *E. edulis* populations have declined due to intense palm-heart harvesting (Galetti and Fernandez, 1998). Each individual produces between one and five infructescences annually that may bear over 3000 fruits each (Mantovani and Morellato, 2000). Fruits are globose with a single rounded seed (13.5 mm length, 14.2 mm width; Pizo et al., 2006) covered by a thin layer of black pulp when mature. In the study region, fruit maturation generally extends from April to September, peaking in June–July (Galetti et al., 1999; Rother, 2006). Fruits of *E. edulis* are eaten and its seeds dispersed by several bird species (Galetti et al., 1999; Fadini et al., 2009).

S. guianensis (Aubl.) Benth. (Elaeocarpaceae) is one of the tallest arboreous species in the Atlantic rainforest (Sanchez, 1994), reaching heights above 20 m (D.C. Rother, pers. observ.). Fruit maturation generally extends from December to March (Zipparro and Morellato, 2005). Its fruit is a dry capsule that dehisces upon ripening to expose a single seed (10 mm × 6 mm) covered by a red aril attractive to frugivorous birds (Pinheiro and Ribeiro, 2001).

V. bicuhyba (Schott) Warb. (Myristicaceae) is a dioiceous tree reaching heights between 15 and 30 m. Fruit maturation extends from July to October (Zipparro and Morellato, 2005). Fruits of *V. bicuhyba* are dehiscent capsules containing a single seed (21.4 mm × 15.0 mm) surrounded by a lipid-rich aril that attracts medium to large frugivorous birds such as toucans and cotingas (Rodrigues, 1980; Galetti et al., 2000).

Seed rain and seedling plots

Seed traps of 0.25 m^2 spaced by at least 20 m from each other were randomly set in each kind of stand avoiding edge areas. An equal number of similar-sized seedling plots were located beside each seed trap, totaling 61 seed traps and 61 seedling plots, with 30 points at NB and 31 at B stands. Four distinct patches of bamboo were used for setting the 31 seed traps and experimental plots in B stands. While relatively small sampling units such as those used here can overestimate the actual value of seed/seedling limitation (Norden et al., 2007; Kobe and Vriesendorp, 2009), they allow a fine-grained assessment of a number of mortality factors (see below) that would be very difficult to quantify over larger experimental units. Seed traps were wooden boxes lined with a fine fabric (1 mm mesh) and suspended 10 cm above the ground to minimize seed loss between successive censuses. Seeds were collected monthly (from November 2007 to January 2009) and subsequently counted and identified to the lowest possible taxonomic level. Seedlings were individually marked with a numbered tag and identified monthly from January 2008 to November 2008. This design was chosen to evaluate how seed rain density is correlated with the realized establishment limitation (the proportion of sites receiving seeds at which establishment does not occur; Müller-Landau et al., 2002).

Seed addition experiments

We conducted seed addition experiments by combining two factors, seed density and seed predation, in replicated experimental plots with two levels each. For the Control level we used the naturally occurring seed density of each species, as determined by the concurrent seed rain study. Seed addition ("Addition treatment") involved sowing an augmented density of seeds, the level of which was determined relative to the Control. In the Addition treatment the density of seeds naturally occurring in the seed rain was increased three-fold for all species except *V. bicuhyba*. Low seed availability of *V. bicuhyba* allowed only a two-fold increase of the naturally occurring seed rain in the Addition treatment of this species. For *E. edulis*, four and seven seeds were used in Control, and 12 and 21 seeds in Addition treatment for B and NB stands, respectively. For *S. guianensis*, two and six seeds were used for Control and Addition treatments, respectively, in both B and NB stands. Finally, for *V. bicuhyba*, two and four seeds were used for Control and Addition treatment at each type of stand. The influence of seed predation upon seedling establishment was tested using wire cages (1.2 cm mesh size, 25 cm × 25 cm) that protected the seeds from vertebrate seed predators (Excluded treatment), with the survival of protected seeds being contrasted with unprotected seeds (Open treatment).

Treatments were arranged in 40 100 × 100 cm experimental units or blocks, each one containing a full combination of the two treatment factors: seed density and seed predation. Twenty blocks were placed randomly at B and NB stands, with replicates spanning four different bamboo stands. Leaf litter was removed from each block area and seeds of each species were sown during their natural seed dispersal period. Seeds of *E. edulis* were sown in July 2007, *S. guianensis* in December 2008, and *V. bicuhyba* in September 2008, which corresponded to species distinct dispersal and germination periods in the field. Seed viability was tested prior to sowing by floating on water. Only potentially viable seeds (i.e., those that did not float) were used, so that seeds evidently damaged were discarded, allowing a conservative estimate of germination success. Each seed was marked with a small stick to facilitate relocation in subsequent monthly census after the initial sowing. Data on seed predation, seedling emergence, herbivory and seedling survival were collected monthly for each species until seedlings reached 15 cm high.

Data analysis

Regeneration bottlenecks

Transition probabilities (TP) were used to quantify the survival probability at each stage involved in regeneration and the cumulative probability of a seed becoming an established seedling. Also, TP analysis provides information about the spatial distribution of recruitment considering B and NB stands (e.g., Rey and Alcántara, 2000). To estimate TP, we used data from seed traps and seedling plots to evaluate: (1) total seed rain, (2) dispersed seeds, (3) emerging seedlings, (4) established seedlings, and (5) total seedling recruitment. "Total seed rain" was the total number of seeds (i.e., dispersed seeds plus seeds partially covered by pulp or aril) collected in the sampled area (i.e., B and NB stands pooled), and refers to any fruit/seed manipulated by an animal frugivore; it thus aims at quantifying the initial seed rain just after successful dissemination by animals. "Dispersed seeds" corresponded to the intact seeds without their pulp or aril collected in seed traps, thus estimating successful handling and dispersal by frugivores (defecated/regurgitated seeds). As soon as seedlings emerged, they were

considered as "emerging seedlings", while seedlings surviving until the last census were considered as "established seedlings". Finally, "total seedling recruitment" is the sum of all seedlings recorded at B and NB stands. TP from dispersed seeds to total seed rain was calculated by dividing the number of seeds recorded in a particular stand by the total seeds recorded in both stands. Subsequent TPs were calculated by the number of propagules in a stage divided by the number of propagules from the previous stage recorded in the same stand.

Diagrams of the recruitment dynamics were built for each plant species showing both the TP at each stage and the cumulative recruitment probability for each stand. To construct these diagrams, data from seed traps and seedling plots were used. In some cases, the number of seedlings in the plots exceeded the number of initial seeds recorded in the corresponding seed trap. In these cases, we used the estimated germination rate obtained from the seed addition experiments to retrospectively-calculate the number of seeds expected to generate the recorded number of seedlings. Thereafter we divided the recorded number of emerging seedlings by the germination rate obtained from the mean value of the addition and control treatments of the open replicates in the seed addition experiments.

Factors limiting recruitment

From the seed addition experiments we estimated the number of seeds and seedlings lost due to biotic and abiotic factors for each treatment within each stand type. Firstly, we calculated the proportion of seeds or seedlings affected by a given mortality factor (M_1, ..., M_n). Secondly, we obtained the probability of survival after the action of the mortality factor as $1 - M_n$. Then the cumulative probability was obtained as the product of the transition probabilities of the specific process involved at each stage.

The analysis included a comparison of recruitment stages in B and NB stands and the factors that could result in demographic bottlenecks. In the transition from seeds to the early seedling stage (emerging seedlings), we considered four categories representing demographic mortality factors on recruitment: (1) predation, (2) pathogens, (3) lost to drought, and (4) removal. "Predation" refers to seed loss by herbivore damage to the endosperm and embryo tissues; "Pathogens" accounts for seed loss due to fungal activity; "Lost to drought" includes seed loss due to desiccation, and "Removal" refers to missing seeds that were removed by mammals (especially rodents), or disappeared due to mammal trampling or rainfall runoff. In this case, the extent to which "Removal" represents seed dispersal is unknown because we did not evaluate secondary dispersal. Some of the "removed" seeds might have been cached or buried and some can emerge lately (Forget, 1991, 1993), resulting in slight mortality overestimates.

For the transition from emerging seedlings to the established seedling stage, we considered the following factors: (1) herbivory, (2) pathogens, (3) lost to drought, and (4) others. "Herbivory" is the loss of a seedling due to herbivore damage on the meristem tissues; "Pathogens" is the seedling loss due to fungal activity; "Lost to drought" is the seedling loss to water deficit in the soil, and "Others" includes seedling loss due to mammal trampling or unknown causes.

To determine the overall mortality of propagules from dispersed seed to established seedling, we evaluated the relative importance of each mortality factor by regression of the total number of seeds germinating and seedlings established on the loss attributed to each of the mortality factors. We fitted a multiple regression model with library relaimpo (Grömping, 2006) in R package, version. 2.9.2. We used these regression models to quantify the relative importance of each individual regressor (mortality factor) to the overall recruitment at the early stage (number of emerging seedlings)

and to the total loss of propagules throughout the recruitment period (up to the final number of surviving seedlings), i.e., the "seed to early seedling" and "early seedling to established seedling" stages, and which of all regressors contributed to the full model R^2 (Grömping, 2006). The analysis yields a "natural" decomposition of the linear regression model R^2 and provides metrics for the relative influence of each predictor on the dependent variable, as well as bootstrap estimates for the confidence intervals of the metrics (Grömping, 2006). This analysis was performed in two ways. First, mortality levels for each factor were regressed on the number of seeds germinating in each plant species at B and NB stands. Second, the mortality levels for each factor were regressed on the total loss of propagules during the recruitment of the three species in the stands.

Generalized models were used to estimate the significance of treatment effects on overall seedling emergence and seedling survival of each species. To perform this analysis, the number of emerging seedlings alive in each plot was related to the initial number of seeds sown and grouped by stand type, seed addition treatment, and exclusion treatment. We used zero-inflated count models, a special procedure for data with an excess frequency of zeroes such as the type of data typically obtained when using seed traps and seedling plots. We used a log link function and we also specified a negative binomial distribution for this type of data, which had both a super-excess of zeroes and also some sampling points where the number of seeds or seedlings is extremely high (i.e., a 'fat-tailed' distribution of the number of seeds/trap and/or the number of seedlings/plot). Therefore, we fitted the data of number of emerging seedlings and number of seedlings surviving per replicate treatment to test differences between B and NB stands. For this analysis, the library pscl (Jackman, 2009) in R package, version 2.9.2 was used (R Development Core Team, 2009). The zero-inflated count models provided a superior fit to the alternative negative binomial model (library MASS; R package) as indicated by a Vuong test. We report the results from the zero-inflated models as in all cases but one (the fit of the final number of surviving *S. guianensis* seedlings) they resulted in better fits than the regular negative binomial model.

Results

Regeneration bottlenecks

Comparing the three species, *E. edulis* presented a higher seed density (=18.6 ± 0.8 seeds m^{-2}; mean ± SD) than *S. guianensis* and *V. bicuhyba* (8.1 ± 1.0 and 0.79 ± 0.1 seeds m^{-2}, respectively) (Fig. 1). While the seed rain of *E. edulis* is relatively widespread (21.3% of the traps had at least one seed recorded; 11.5% of the plots with at least one seedling surviving), *S. guianensis* and *V. bicuhyba* had more restricted seed dissemination (18.0% and 11.5% of the traps with at least one seed, respectively; 3.3% and 1.6% of the plots with at least one seedling surviving, respectively).

The three species differed when considering the dispersal and recruitment patterns at B and NB stands (Table 1). We recorded a significantly greater *E. edulis* seed density in NB stands, whereas B stands had increased emergence and seedling survival (Fig. 1A). For *S. guianensis*, seed dispersal in B stands was extremely limited. Only 0.8% of the total *S. guianensis* seed rain (8.1 ± 1.0 seeds m^{-2}) in the permanent plot was dispersed to B stands, resulting in 0.1 ± 0.03 dispersed seeds m^{-2}. Therefore, seed dispersal was a potentially critical phase for *S. guianensis* regeneration in B stands (Fig. 1B). The total *V. bicuhyba* seed rain was very low in both kinds of stands. At B stands, however, *V. bicuhyba* seeds had a 75% dispersal probability, but this did not translate into significant differences in the seed rain. On the other hand, NB stands
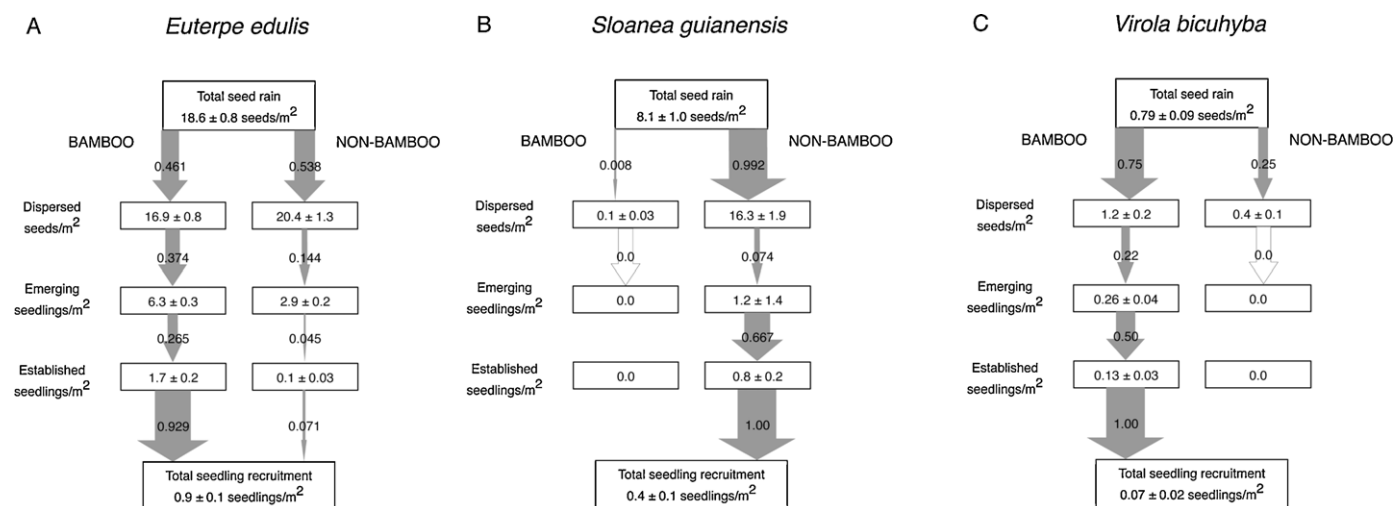
Fig. 1. Diagram of the recruitment dynamics of *Euterpe edulis* (A), *Sloanea guianensis* (B), and *Virola bicuhyba* (C) showing the transition probabilities at each stage and the cumulative probability for bamboo and non-bamboo stands.

showed a collapse in the *V. bicuhyba* regeneration cycle by a failure of seedlings to emerge (Fig. 1C).

Differences in the final recruitment at B and NB stands resulted from the cumulative action of stage-specific transition probabilities that markedly differed between stands and among species (Fig. 1). The cumulative probability of recruitment (Fig. 2) indicates that *E. edulis*, *S. guianensis* and *V. bicuhyba* seeds had a low probability of reaching the seedling survival stage in both B and NB stands. Interestingly, there was a clear separation between the trends of cumulative recruitment in "Open" and "Closed" treatments, independently of the stand type. The exclusion of post-dispersal seed predators, herbivores, and mammal trampling or removal in the Closed treatments resulted in a higher probability of survival until the stage of established seedlings which initiates in the transition probability number 5 in Fig. 2. The difference between Open and Excluded treatments was more marked for *S. guianensis*, whose seed survival rate increased to 10% in the Excluded treatment (Fig. 2).

Mortality factors limiting recruitment

The relative importance of each mortality factor to the number of seeds germinating is shown in Table 2. Among the species studied, seed germination of *S. guianensis* was more strongly suppressed by the "Removal" factor. This could have been caused by rodent activity at B stands (with a relative contribution to $R^2 = 0.99$). At NB stands, all mortality of *S. guianensis* was attributed to the "Removal" factor because seeds were completely absent in the first monitoring stage of the experiment.

Table 1

Differences in the density of seeds and seedlings of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in bamboo (B) and non-bamboo (NB) stands.

Stage	*Euterpe*	*Sloanea*	*Virola*
Seeds dispersed	B < NB[*]	B < NB[**]	B > NB[NS]
Seedling emergence	B > NB[*]	B < NB[~]	B > NB[NS]
Seedling survival	B > NB[*]	B < NB[NS]	B > NB[NS]

Significances of the differences in densities between B and NB stands were tested with a generalized linear model for zero-inflated data:

[*] $P < 0.05$.
[**] $P < 0.01$.
[~] $0.05 < P < 0.10$.
NS, non-significant.

Table 2

Relative importance of each mortality factor to seeds of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* successfully germinating at bamboo (B) and non-bamboo (NB) stands. Values of total R^2 represent percentages of variance explained in the number of seeds germinating accounted for by the combination of all mortality factors; values for each factor indicate the proportional effect (contribution to total R^2 in percentages) of each mortality factor. Mortality factors are normalized to sum to 100%.

Factors	*Euterpe*		*Sloanea*		*Virola*	
	B	NB	B	NB	B	NB
Removal	73	73	99	[a]	57	73
Predation	16	19	1	[a]	43	27
Pathogens	11	8	–	–	–	–
Total R^2	61.4	65.7	71.9	[a]	65.1	77.1

[a] All mortality was attributed to the "removal" factor for *Sloanea* in non-bamboo stands.

Seed loss caused by herbivory damage to the endosperm and embryo tissues had a limited contribution for pre-germination losses in all three species. *V. bicuhyba* presented high values for the "Predation" factor, especially at B stands (relative contribution to $R^2 = 0.43$). Seed loss to fungal activity was recorded only for *E. edulis* seeds and had a low contribution to total seed mortality in both B and NB stands. Overall, the "removal" effect resulted in most pre-germination losses.

The relative importance of each mortality factor to the total loss of propagules during the recruitment showed that the factors varied in degree of importance for each species as well as according to stand type (Table 3). For *E. edulis* and *V. bicuhyba*, "Removal" and "Others" were the most relevant factor that contributed to early seed mortality and mortality of established seedlings, respectively, in both B and NB stands (relative contribution of $R^2 > 0.15$ and 0.30 for these two stages, respectively). This combination of mortality sources in fact contributed to approximately one third of the overall mortality of any species at both stands, with a slight trend for a more limited effect (<0.28 in all cases) in the seed to early seedling transition (Table 3). Losses caused by seed predation and seedling herbivory were sizeable but quite variable among species, stands, and for the two transitions considered, with no clear patterns. However, the relative contribution of losses to predation was more limited for the small-seeded *S. guianensis* (0.03) and greater for the large-seeded *E. edulis* and *V. bicuhyba* (>0.10). In *E. edulis* most mortality was caused by losses to "Removal", "Others" and
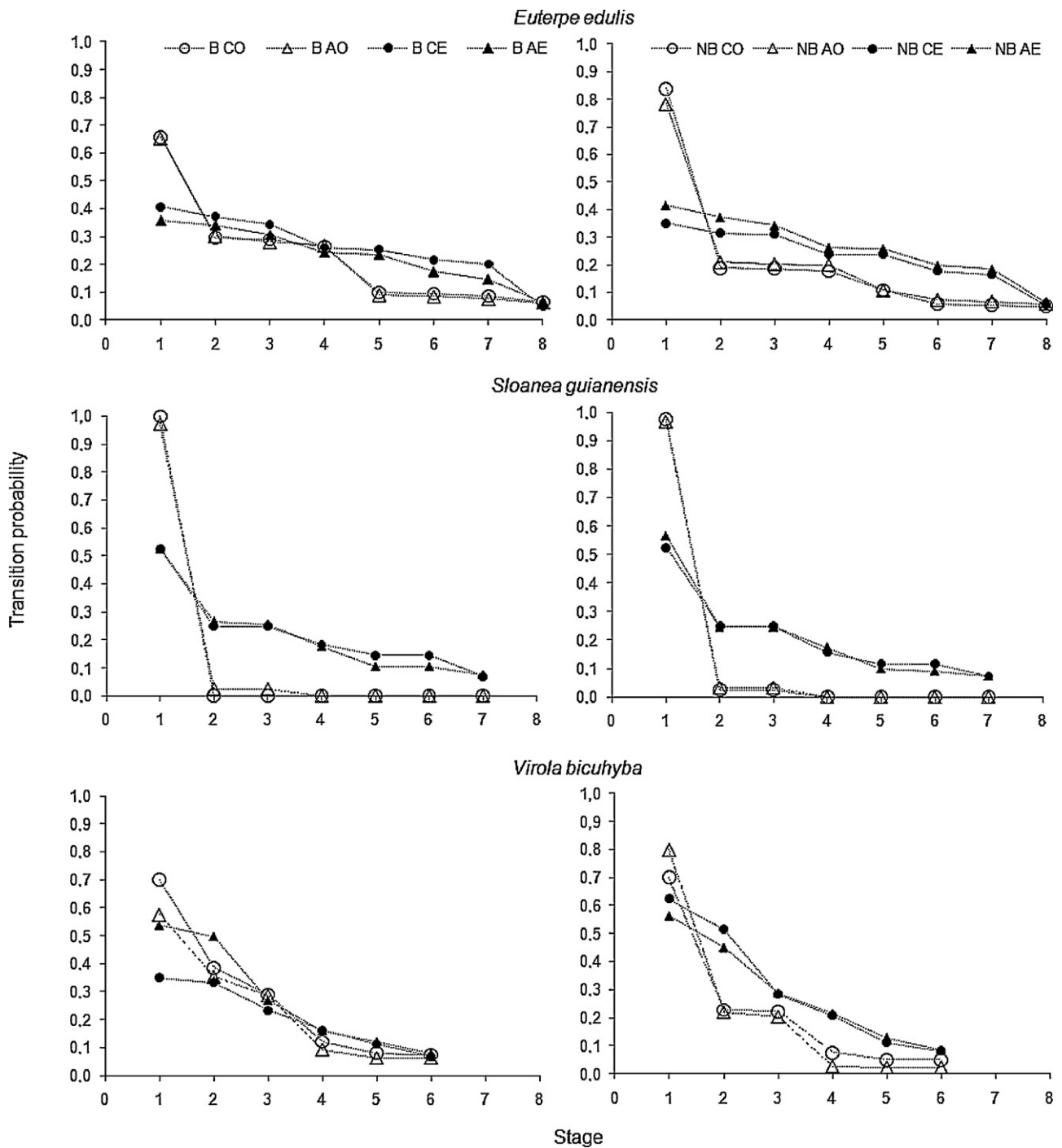
Fig. 2. Cumulative probabilities of a seed reaching the seedling survival stage under demographic bottlenecks in the regeneration cycle. Probabilities were estimated from the initial number of seeds sown in each treatment combination. Numbers in the abscissa axis represent approximately sequential stages where the action of different mortality factors on "seed to early seedling" and "early seedling to established seedling" transitions takes place. For *Euterpe edulis*, to early seedling: (1) germination, (2) removal, (3) predation, (4) pathogens, and to survivor seedlings: (5) others, (6) herbivory, (7) pathogens, (8) final survival. For *Sloanea guianensis*, to early seedling: (1) germination, (2) removal, (3) pathogens, and to survivor seedlings: (4) others, (5) herbivory, (6) lost to drought, (7) final survival. For *Virola bicuhyba*, to early seedling: (1) germination, (2) removal, (3) predation, and to survivor seedlings: (4) others, (5) herbivory, (6) final survival. Panels on the left show the trends for bamboo stands, and those on the right refer to non-bamboo stands. Open symbols indicate Open treatments (Add or Control) and closed symbols indicate Excluded treatments (Add or Control). For bamboo stands: (BCO) control open, (BAO) add open, (BCE) control excluded and (BAE) add excluded. For non-bamboo stands: (NBCO) control open, (NBAO) add open, (NBCE) control excluded and (NBAE) add excluded.

"Herbivory", and in *V. bicuhyba* the relative contribution of the different mortality causes was greater, with most effects in any stand having ~0.25–0.35 relative contribution (Table 3).

In B stands, mortality of *S. guianensis* propagules in the transition from seed to early seedling stage was largely dependent on

the "Removal" factor. This factor had a high relative importance, indicating that the removal by rodents or other factors was the most important cause of *S. guianensis* seed loss at B stands. From early seedling to the established seedling stage, propagule loss was largely caused by "Others" (0.30) and "Lost to drought" (0.27)

Table 3
Relative importance of each mortality factor to the total loss of propagules during the recruitment of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in bamboo (B) and non-bamboo (NB) stands. Values of total R^2 represent percentages of variance explained in the number of seeds or seedlings lost (total mortality) caused by the combination of all mortality factors. Values for each factor indicate the proportional effect (contribution to total R^2 in percentages) of each mortality factor to overall mortality. Mortality factors are normalized to sum to 100%.

Stage	Factors	Euterpe		Sloanea		Virola	
		B	NB	B	NB	B	NB
Seed to early seedling	Removal	15	26	40	[a]	31	28
	Predation	10	26	3	[a]	20	26
	Pathogens	3	3	–	–	–	–
Early seedling to established seedling	Others	38	34	30	[a]	35	30
	Herbivory	19	7	–	–	14	16
	Pathogens	15	4	–	–	–	–
	Lost to drought	–	–	27	[a]	–	–
	Total R^2	48.4	47.1	70.5	[a]	48.4	42.8

[a] All mortality was attributed to the "removal" factor for *Sloanea* in non-bamboo stands.

factors. In NB stands, all *S. guianensis* mortality was attributed to the "Removal" factor because seeds were completely absent in the first monitoring most likely due to runoff.

Seed addition experiments and recruitment limitation

In *E. edulis*, the regression model for the number of emerging seedlings was significant for the three main effects (stand type, exclusion, seed addition), and the three-way interaction (stand type × exclusion × seed addition) (Table 4). Hence, the number of seeds germinating depended significantly on the stand type and on both the exclusion and addition treatments, but always considering the type of stand. This result is mainly due to the greater percentage of emerged *E. edulis* seedlings in B stands, where the exclusion treatment was highly effective in reducing mortality (Table S1 in Supporting Information; Fig. 3). However, the exclusion treatment did not significantly influence the final recruitment of established *E. edulis* seedlings. It seems that seedling mortality diluted the effect of exclusion and made the final recruitment similar to open treatments and to those where seed predators were excluded.

There were also differences between stands, with B stands showing a greater number of surviving seedlings. The addition treatment was also highly significant in determining the final number of established seedlings. Both the addition and exclusion treatments showed effects that were dependent on stand type, with more marked positive effects on final recruitment in B stands (Fig. 4).

The regression model for the number of emerging seedlings of *S. guianensis* showed a significant effect of seed addition and predator exclusion (Table 4). The results for *S. guianensis* showed an absence of emerging seedlings in the open control treatment in B stands, and an absence of final recruitment in Open treatments at both stands (Table S1, Fig. 3). Thus, these findings showed a highly significant effect of the exclusion treatment on both early seedling emergence and later establishment. This result demonstrates that, when protected, seeds of *S. guianensis* had a much higher probability of emerging and surviving to establishment in both stand types (Figs. 3 and 4). Therefore, our findings show that the influence of seed addition in increasing seedling establishment of *S. guianensis* is limited when seeds are exposed to predators and herbivores.

Similarly to *S. guianensis*, we did not obtain emerging seedlings of *V. bicuhyba* in the NB stand open control treatment (Table S1, Fig. 3). On the contrary, seeds in the Excluded treatment had higher probabilities of reaching the emerged seedling stage, especially at NB stands (Table S1, Fig. 3).

In sum, the Addition treatment increased significantly the number of surviving seedlings for all three species. However, for *S. guianensis* and *V. bicuhyba* this effect strongly depended on predator/herbivore exclusion, as both species experienced very high seed and seedling losses. When protected from vertebrate action, the probability that propagules reached the emerging seedlings stage increased for all three species.
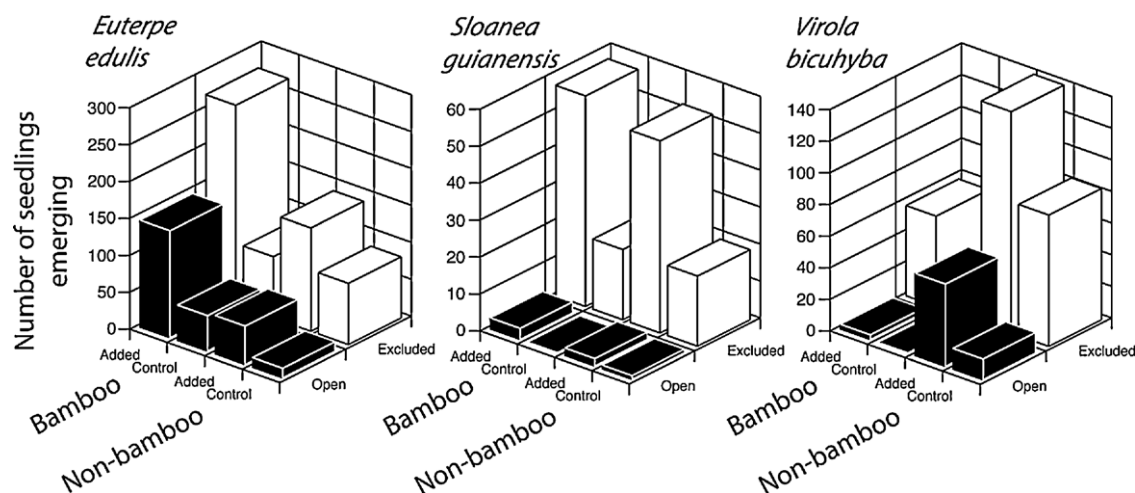
Table 4
Summary of GLM model fits (with zero-inflated distributions) for the early (number of emerging seedlings) and late (number of established seedlings) recruitment success of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in bamboo and non-bamboo stands.

	Euterpe		Sloanea		Virola	
	χ^2, df	Effect significance	χ^2, df	Effect significance	χ^2, df	Effect significance
Emerging seedlings	154.0*** 3, 7	M***; E***; A*** M·E·A*	57.3*** 3, 11	E**; A* – –	35.8*** 3, 11	– M·E~ M·E·A*
Established seedlings	114.0*** 3, 7	M*; E~; A*** M·A***; M·E*	37.5** 3, 11	All[NS]	31.6** 3, 11	All[NS]

Effects – M: microhabitat (stand type; bamboo or non-bamboo); A: seed addition; E: exclusion of post-dispersal seed predators and vertebrate herbivores. Treatment significance indicates the significant effects and one-, two-, and three-way interaction terms (indicated by dots) for each recruitment variable and species.
Significance of the likelihood-ratio tests comparing the fitted model with a null model and specific tests for each effect and interaction. Only the significant terms are shown:

* $P \leq 0.05$.
** $P < 0.001$.
*** $P < 0.0001$.
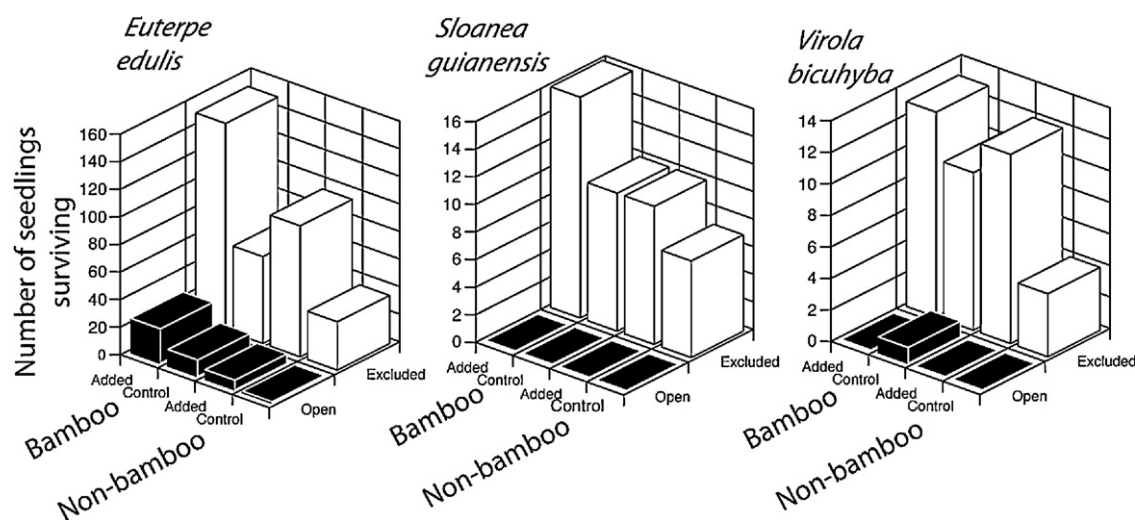~ $0.05 < P < 0.10$.
NS, non-significant.

Fig. 3. Number of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* emerging seedlings in bamboo and non-bamboo stands in relation to a combination of seed addition treatment ("Added" vs. "Control"), and the exclusion of post-dispersal seed predators ("Excluded" vs. "Open").

Fig. 4. Number of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* surviving seedlings in bamboo and non-bamboo stands in relation to a combination of seed addition treatment ("Added" vs. "Control"), and the exclusion of post-dispersal seed predators ("Excluded" vs. "Open").

Discussion

Our findings come from the use of two complementary approaches to assess recruitment limitation in tropical forests: first, we used an observational procedure to identify key stages potentially limiting recruitment and stage-specific transition probabilities. Our data on three arboreal species show consistencies and inconsistencies among species. Second, we combined this analysis with seed addition and herbivory exclusion experiments, linking findings with the previously identified bottlenecks. We evaluated the relative roles of seed dispersal and recruitment limitation in successful seedling establishment, and identified regeneration bottlenecks operating in the habitat mosaic formed by bamboo stands.

Demographic bottlenecks: an observational approach

Our results highlight the crucial role of landscape heterogeneity in determining seed to seedling regeneration limitation in tropical woody species. We found that stands dominated by bamboos in the Atlantic rainforest can influence the successful recruitment of woody species. Density of propagules and recruitment stage in

which propagules are more limited can vary among species and with stand type (microhabitat type). In addition, at each stage, the propagule density varies with plant species, being influenced by factors affecting the suitability of establishment sites (Müller-Landau et al., 2002; Jordano et al., 2004). However, susceptibility to predation can be more crucial than microhabitat differences in determining survival of some species (Molofsky and Fisher, 1993). While observational data from seed traps and seedling plots can help in assessing recruitment limitation patterns (Müller-Landau et al., 2002), when combined with seed addition experiments under controlled conditions in distinct microhabitats they can be conclusive in identifying key stages that limit establishment.

The recruitment dynamics of *E. edulis* represented by total seed rain and dispersed seed density increased in NB stands, whereas B stands presented greater densities of emerging and established seedlings. Therefore, if dispersal is not a problem for *E. edulis* seeds in NB, its success in the subsequent establishment stages is strongly constrained by post-dispersal mortality factors in this stand. Insects and rodents cause significant post-dispersal predation of *E. edulis* seeds (Pizo and Simão, 2001). In NB stands, the proportion of propagule losses in the transition from seed to early

seedling stage was similar between "removal" and "predation" factors, which agrees with Allmen et al. (2004) who studied predation of *E. edulis* seeds at a nearby site. Bamboo stands, on the other hand, can significantly limit the seed rain of this palm (e.g., due to their distinct physiognomic characteristics that do not favor the presence of avian frugivores), but provide good conditions for germination and seedling establishment (e.g., due to limited activity of post-dispersal seed predators or limited seed removal in this stand type). These more favorable conditions for early seedling establishment could however occur just at the stand edges, where most seed rain is concentrated and the unfavorable effects of bamboo litter are most likely reduced.

Regarding *S. guianensis*, seed dispersal was extremely limited at B stands. Despite both stands showing marked propagule losses, mortality factors contributed to greater propagule losses in the initial life cycle of *S. guianensis* in NB than B stands. The stage of established seedling of *S. guianensis* was particularly limited at NB stands, where the probability of recruitment in the preceding stages was clearly high (Fig. 1). It seems that plant–insect herbivores interactions are preserved in NB, and that demographic bottlenecks are more intense in this environment during the transition from seed to early seedling. NB stands appear to have microhabitats that may favor individuals within the *S. guianensis* population. Other studies have shown that seed survival might differ among distinct microhabitats if seed predators use them non-randomly (Kiltie, 1981; Willson, 1988; Whelan et al., 1991). In addition, a survey of results reported in the literature showed no consistent habitat or microhabitat patterns in seed survivorship (Willson, 1988). In wet forests, the amount and seasonality of rainfall varies strongly. Drought periods may cause plant stress and consequently decrease seedling survival (Engelbrecht et al., 2005). However, drought was not an important mortality factor for seedlings of any studied species in both stands.

Leaf litter can influence seed and seedling performance by reducing soil temperature and water evaporation, which can result in increased local humidity or reduced rain to soil water infiltration (Santos and Válio, 2002). The influence of leaf litter varies during the first year of the life of some species, inhibiting initial emergence but, at the same time, enhancing early seedling survival (Ibáñez and Schupp, 2002). Thus, leaf litter may affect seeds on the forest floor by increasing their predation rate, altering germination patterns (Schupp, 1988; Molofsky and Augspurger, 1992; Santos and Válio, 2002), and seedling development (Santos and Válio, 2002). With regard to *S. guianensis* recruitment, leaf litter removal when the seed addition experiment was set may have facilitated location of seeds by predators and therefore contributed to their removal, as suggested by Zipparro and Morellato (2005). On the other hand, the leaf litter that naturally accumulated at both stands during the experiment was not removed. We know that B stands accumulate more litter than NB stands (Rother, 2006). Thus, we would not expect to find higher seedling density of *S. guianensis* in B because small seeds are better adapted to surviving in sites with low amounts of litter (Gross, 1984; Molofsky and Augspurger, 1992; Kostel-Hughes et al., 2005).

For shade-tolerant species such as *S. guianensis*, survival depends more on biotic than on abiotic conditions (Molofsky and Fisher, 1993). In contrast, seedlings from larger seeds have a store of provisions that enhances establishment under adverse conditions (Leishman and Westoby, 1994), as in sites with a thick litter layer (Gross, 1984; Winn, 1985; Leishman and Westoby, 1994). Therefore, large-seeded species such as *E. edulis* and *V. bicuhyba* are expected to perform better in the seed to early seedling transition and achieve higher seedling survival at B stands where leaf litter was higher than NB stands (Rother, 2006).

Previous studies showed that the impact of insects on seed survival of *Virola* spp. was lower than vertebrates (De Steven and Putz, 1984; Asquith et al., 1997; Zipparro and Morellato, 2005). Mammals, particularly rodents, are considered the main predators of *V. bicuhyba* spp. seeds in tropical forests (Notman and Gorchov, 2001; Zipparro and Morellato, 2005; Forget et al., 2006). In the current study, the *V. bicuhyba* life cycle was extremely constrained by seed rain at both B and NB stands. Nevertheless, *V. bicuhyba* seeds in B had a 75% dispersal probability, but experienced considerable loss due to post dispersal events that may be attributed to mammal (especially rodents) removal, mammal trampling, or seed displacement by rainfall (Marthews et al., 2008). Interestingly, there was a total collapse of the *V. bicuhyba* regeneration cycle in NB stands caused by propagule failure after seed dispersal, which may be attributed to biotic factors, mainly insect predation and terrestrial mammal removal or predation. In a nearby site, Zipparro and Morellato (2005) found intense predation on *V. bicuhyba* seeds by a Nitidulidae beetle, but noted that predation by vertebrates was the main cause of seed mortality.

The exclusion of post dispersal mortality effects dramatically increased survival up to the established seedling stage (i.e., demographic transition #5, Fig. 2). This key effect could lead to increased regeneration, as shown by the response of *S. guianensis*. Therefore the action of vertebrate herbivores and seed predators makes all species susceptible to narrowing demographic bottlenecks throughout the course of the regeneration cycle. Previous studies have shown that predation of unprotected seeds reduced seedling abundance and consequently recruitment in tropical forests (De Steven and Putz, 1984; Sork, 1987; Schupp, 1990; Asquith et al., 1997; Notman and Gorchov, 2001; Zipparro and Morellato, 2005). Our results indicated that seeds disappeared before germinating. Mammal (especially rodent) removal, mammal trampling or seed displacement by rainfall were more important mortality agents than pathogens, being the main causes of seed and seedling reduction in all species at both stands. This assertion is supported by the fact that cage-protected seeds survived better and produced more seedlings than unprotected seeds. Biotic factors, therefore, severely limited the early recruitment of *E. edulis*, *S. guianensis* and *V. bicuhyba* at the study site irrespective of stand type.

Factors limiting recruitment: the experimental approach

When combined with a quantitative assessment of transition probabilities, seed addition experiments can be invaluable to evaluate factors limiting recruitment (Clark et al., 2007). For the studied species, an increase in initial seed rain density resulted in higher recruitment at both stands, unequivocally identifying a significant dispersal limitation. Moreover, the addition treatment increased the number of emerged seedlings and improved seedling survival for all three species. This shows that seedling establishment is a more limited stage than seed availability or survival, which contrasts with Clark et al. (2007). These authors found that establishment limitation is stronger than seed limitation because most added seeds fail to recruit to the seedling stage.

At both stands there was no spatial concordance in different phases of the life cycle. Nevertheless, seeds of the three studied plant species had a low probability of reaching the established seedling stage except under protected conditions. Plants experience strong pressure from the feeding and trampling activities of herbivores, which often causes a marked limitation of regeneration (Plumptre, 1993). Although unprotected sites were susceptible to narrowing demographic bottlenecks throughout the course of the regeneration cycle, the highest probability of seed and seedling survival in the addition treatment resulted in low limitation in both stands for the three species. This finding points to the central role

of dispersal limitation resulting from a failure of enough seeds to reach specific sites with profound effects on the final stages of establishment.

Regeneration success can indicate the extent to which a specific microhabitat represents a suitable site and how this varies according to species. The potential regeneration patches in different microhabitats can be envisioned as a gradient of variable recruitment probabilities between the "unsafe" and "safe" extremes. The most favorable stands for seeds and seedlings of *E. edulis* and *V. bicuhyba* were bamboo-dominated patches, which represented the least favorable for *S. guianensis* individuals. Therefore, absence of bamboos favors *S. guianensis* recruitment. The positive effects for *E. edulis* and *V. bicuhyba* might be associated to bamboo patch size and/or edge effects, for instance if the edge of bamboo stands is favored by frugivores after feeding on nearby fruiting individuals. Our seed rain data support this theory for *V. bicuhyba* but not for *E. edulis*. However, for both species, bamboo stands facilitated germination success and seedling emergence.

Bamboo effects on the early recruitment of non-bamboo species are therefore species-specific. Nevertheless, negative effects appear to be more prominent at larger sized classes and later stages of plant recruitment, mainly due to physical damage caused by litter and culms that fall on saplings and cause their mortality (Griscom and Ashton, 2003). Bamboo growth dynamics provide an environment where saplings and young trees within the bamboo stand have a high probability of being physically damaged (Griscom and Ashton, 2003). Therefore, an early facilitation of the germination and seedling emergence (e.g., due to edge effects in the bamboo stand) can switch to negative influences at later stages when the bamboo patch expands and the recruits get trapped in a large bamboo-covered area. Experimental research is necessary to evaluate plant survival in the subsequent stages (e.g., older saplings) in order to test the physical effects of bamboo on the final recruitment.

Our results indicate that the early recruitment of the studied plant species in the Atlantic rainforest can be extremely patchy, suggesting a far-reaching influence of the heterogeneity created by successional bamboo patches. While the seed trap data suggested pervasive seed limitation for the three species studied, the experimental analysis and monitoring of subsequent stages indicated a very heterogeneous outcome in terms of recruitment prospects depending on the species and stand type. The combination of observational monitoring of the seed rain and the experimental analysis of post-dispersal seed predation and seedling establishment proved to be essential for understanding the delayed consequences of dispersal limitation processes in this forest.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2012.12.004.

References

Allmen, C., von Morellato, L.P.C., Pizo, M.A., 2004. Seed predation under high seed density condition: the palm *Euterpe edulis* in the Brazilian Atlantic Forest. J. Trop. Ecol. 20, 471–474.

Araujo, L.S., 2008. Padrões e condicionantes da dinâmica da paisagem na floresta com bambus do Parque Estadual Intervales, SP. Ph.D. Thesis, Escola Superior de Agricultura Luiz de Queiroz/USP, Piracicaba, Brazil.

Asquith, N.M., Wright, S.J., Clauss, M.J., 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78, 941–946.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., Hillerrislambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. Am. J. Bot. 86, 1–16.

Clark, C.J., Poulsen, J.R., Levey, D.J., Osenberg, C.W., 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. Am. Nat. 170, 128–142.

Custódio-Filho, A., 2002. A floresta ombrófila densa em diferentes altitudes no Parque Estadual Carlos Botelho, São Paulo, Brasil. Ph.D. Thesis, São Paulo University, São Paulo, Brasil.

DAEE/SP, 2009. Banco de dados pluviométricos do Estado de São Paulo. http://www.daee.sp.gov.br/hidrometeorologia/bancodedados.htm

Dalling, J.W., Muller-Landau, H.C., Wright, S.J., Hubbell, S.P., 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. J. Ecol. 90, 714–727.

De Steven, D., Putz, F.E., 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. Oikos 43, 207–216.

Dias, A.C., 2005. Composição florística, fitossociologia, diversidade de espécies arbóreas e comparação de métodos de amostragem na Floresta Ombrófila Densa do Parque Estadual Carlos Botelho/SP, Brasil. Ph.D. Thesis, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Piracicaba.

Engelbrecht, B.M.J., Kursar, T.A., Tyree, M.T., 2005. Drought effects on seedling survival in a tropical moist forest. Trends Ecol. Evol. 19, 312–321.

Fadini, R.F., Fleury, M., Donatti, C.I., Galetti, M., 2009. Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm. Acta Oecol. 35, 188–196.

Forget, P.M., 1991. Comparative recruitment patterns of two non-pioneer canopy species in French Guiana. Oecologia 85, 434–439.

Forget, P.M., 1993. Post-dispersal predation and scatter hoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. Oecologia 94, 255–261.

Forget, P.M., Milleron, T., Feer, F., Henry, O., Dubost, G., 2006. Effects of dispersal pattern and mammalian herbivores on seedling recruitment for *Virola michelii* (Myristicaceae) in French Guiana. Biotropica 32, 452–462.

Galetti, M., Fernandez, J.C., 1998. Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. J. Appl. Ecol. 35, 294–301.

Galetti, M., Zipparro, V., Morellato, P.C., 1999. Fruit phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic forest of Brazil. Acta Oecol. 5, 115–122.

Galetti, M., Laps, R., Pizo, M.A., 2000. Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. Biotropica 32, 842–850.

García, D., Obeso, J.R., Martínez, I., 2005. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? J. Ecol. 93, 693–704.

Gómez-Aparicio, L., Gómez, J.M., Zamora, R., 2007. Spatiotemporal patterns of seed dispersal in a wind-dispersed Mediterranean tree (*Acer opalus* subsp. *granatense*): implications for regeneration. Ecography 30, 13–22.

González-Varo, J.P., Nora, S., Aparicio, A., 2012. Bottlenecks for plant recruitment in woodland remnants: an ornithochorous shrub in a Mediterranean 'relictual' landscape. Perspect. Plant Ecol. Evol. Syst. 14, 111–122.

Griscom, B.W., Ashton, P.M.S., 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. Forest Ecol. Manage. 175, 445–454.

Griscom, B.W., Ashton, P.M.S., 2006. A self-perpetuating bamboo disturbance cycle in a Neotropical forest. J. Trop. Ecol. 22, 587–597.

Grömping, U., 2006. Relative Importance for linear regression in R: the package relaimpo. J. Stat. Softw. 17, 1–27.

Gross, K.L., 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. J. Ecol. 72, 369–387.

Guilherme, F.A.G., Oliveira-Filho, A.T., Appolinario, V., Bearzoti, E., 2004. Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in South-Eastern Brazil. Plant Ecol. 174, 19–36.

Harms, K.E., Wright, S.J., Calderón, O., Hernandez, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404, 493–495.

Harper, J.L., 1977. The Population Biology of Plants. Academic Press, London.

Ibáñez, I., Schupp, E.W., 2002. Effects of litter, soil surface conditions, and microhabitat on *Cercocarpus ledifolius* Nutt. seedling emergence and establishment. J. Arid Environ. 52, 209–221.

Iida, S., 2004. Indirect negative influence of dwarf bamboo on survival of *Quercus acorn* by hoarding behavior of wood mice. Forest Ecol. Manage. 202, 257–263.

Jackman, S., 2009. Pscl: classes and methods for R developed in the political science computational laboratory, Stanford University. Department of Political Science, Stanford University. Stanford, CA. URL: http://pscl.stanford.edu/R package version 1.03.2.

Jordano, P., Herrera, C.M., 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Ecoscience 2, 230–237.

Jordano, P., Pulido, F., Arroyo, J., García-Castaño, J.L., García-Fayos, P., 2004. Procesos de limitación demográfica. In: Valladares, F. (Ed.), Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, EGRAF S.A., Madrid, pp. 229–248.

Kiltie, R.A., 1981. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. Biotropica 13, 141–145.

Kobe, R.K., Vriesendorp, C.F., 2009. Size of sampling unit strongly influences detection of seedling limitation in a wet tropical forest. Ecol. Lett. 12, 220–228.

Kostel-Hughes, F., Young, T.P., Wehr, J.D., 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. J. Torrey Bot. Soc. 132, 50–61.

Leishman, M.R., Westoby, M., 1994. The role of large seed size in shaded conditions: experimental evidence. Funct. Ecol. 8, 205–214.

Lima, R.A.F., Gandolfi, S., 2009. Structure of the herb stratum under different light regimes in the Submontane Atlantic Rain Forest. Braz. J. Biol. 69, 631–637.

Lima, R.A.F., Dittrich, V.A.O., Souza, V.C., Salino, A., Breier, T.B., Aguiar, O.T., 2011. Flora vascular do Parque Estadual Carlos Botelho, São Paulo, Brasil. Biota Neotropica 11. Available at http://www.biotaneotropica.org.br/v11n4/en/abstract?inventory+bn01211042011

Lima, R.A.F., Rother, D.C., Muler, A.E., Lepsch, I.F., Rodrigues, R.R., 2012. Bamboo over-abundance alters forest structure and dynamics in the Atlantic Forest hotspot. Biol. Conserv. 147, 32–39.

Mantovani, A., Morellato, L.P.C., 2000. Fenologia da floração, frutificação, mudança foliar e aspectos da biologia floral do palmiteiro *Euterpe edulis* (Arecaceae). Sellowia 49, 23–38.

Marthews, T.R., Mullins, C.E., Dalling, J.W., Burslem, D.F.R.P., 2008. Burial and secondary dispersal of small seeds in a tropical forest. J. Trop. Ecol. 24, 595–605.

Martínez-Ramos, M., Soto-Castro, A., 1993. Seed rain and advanced regeneration in a tropical rain forest. In: Fleming, T.H., Estrada, A. (Eds.), Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects. Kluwer Academic Publishers, Dordrecht, pp. 299–318.

Mendoza, I., Gómez-Aparicio, L., Zamora, R., Matías, L., 2009. Recruitment limitation of forest communities in a degraded Mediterranean landscape. J. Veg. Sci. 20, 367–376.

Molofsky, J., Augspurger, C.K., 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73, 68–77.

Molofsky, J., Fisher, B.L., 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. Ecology 74, 261–265.

Morellato, L.P.C., Haddad, C.F.B., 2000. Introduction: the Brazilian Atlantic forest. Biotropica 32, 786–792.

Müller-Landau, H.C., Wright, S.J., Calderón, O., Hubbell, S.P., Foster, R.B., 2002. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International, Wallingford, UK, pp. 35–53.

Münzbergová, Z., Herben, T., 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. Oecologia 145, 1–8.

Nelson, B.W., 1994. Natural forest disturbance and change in the Brazilian Amazon. Remote Sens. Rev. 10, 105–125.

Notman, E., Gorchov, D.L., 2001. Variation in post-dispersal seed predation in mature Peruvian lowland tropical forest and fallow agricultural sites. Biotropica 33, 621–636.

Norden, N., Chave, J., Caubère, A., Châtelet, P., Ferroni, N., Forget, P.-M., Thébaud, C., 2007. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. J. Ecol. 95, 507–516.

Pinheiro, F., Ribeiro, J.F., 2001. Síndromes de dispersão de sementes em Matas de Galeria do Distrito Federal. In: Ribeiro, J.F., da Fonseca, C.E.L., Sousa-Silva, J.C. (Eds.), Cerrado: caracterização e recuperação de matas de galeria. Embrapa Cerrados, Planaltina, Brazil, pp. 335–375.

Pizo, M.A., Simão, I., 2001. Seed deposition patterns and the survival of seeds and seedlings of the palm *Euterpe edulis*. Acta Oecol. 22, 229–233.

Pizo, M.A., Allmen, C., von Morellato, L.P.C., 2006. Seed size variation in the palm *Euterpe edulis* and the effects of seed predators on seed germination and seedling survival. Acta Oecol. 29, 311–315.

Plumptre, A.J., 1993. The effects of trampling damage by herbivores on the vegetation of the Parc National des Volcans, Rwanda. Afr. J. Ecol. 32, 115–129.

R Development Core Team, 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.orgS

Rey, P., Alcántara, J.M., 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J. Ecol. 88, 622–633.

Rodrigues, W.A., 1980. Revisão taxonômica das espécies de *Virola* Aublet (Myristicaceae) do Brasil. Acta Amazon. 15, 1–127.

Rother, D.C., 2006. Chuva de sementes e estabelecimento de plântulas em ambientes com bambus na Mata Atlântica. M.Sc. Thesis, Universidade Estadual Paulista, Rio Claro, Brazil.

Rother, D.C., Rodrigues, R.R., Pizo, M.A., 2009. Effects of bamboo stands on seed rain and seed limitation in a rainforest. Forest Ecol. Manage. 257, 885–892.

Sanchez, M., 1994. Florística e fitossociologia da vegetação arbórea nas margens do Rio da Fazenda (Parque Estadual da Serra do Mar, Núcleo Picinguaba, Ubatuba – SP). M.Sc. Thesis, Universidade Estadual Paulista, Rio Claro, Brazil.

Santos, S.L., Válio, I.F.M., 2002. Litter accumulation and its effect on seedling recruitment in a Southeast Brazilian Tropical Forest. Rev. Bras. Bot. 25, 89–92.

Schupp, E.W., 1988. Factors affecting post-dispersal seed survival in a tropical forest. Oecologia 76, 525–530.

Schupp, E.W., 1990. Annual variation in seedfall, post-dispersal predation, and recruitment in a Neotropical tree. Ecology 71, 504–515.

Schupp, E.W., 1995. Seed seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. 82, 399–409.

Schupp, E., Milleron, T., Russo, S., 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey, D., Silva, W., Galetti, M. (Eds.), Seed Dispersal And Frugivory: Ecology, Evolution and Conservation. CAB International, Wallingford, UK, pp. 19–33.

Sork, V.L., 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68, 1341–1350.

Turnbull, L.A., Crawley, M.J., Rees, M., 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88, 225–238.

Wang, B., Smith, T., 2002. Closing the seed dispersal loop. Trends Ecol. Evol. 17, 379–385.

Whelan, C.J., Willson, M.F., Tuma, C.A., Souza-Pinto, I., 1991. Spatial and temporal patterns of postdispersal seed predation. Can. J. Bot. 69, 428–436.

Willson, M.F., 1988. Spatial heterogeneity of post-dispersal survivorship of Queensland rainforest seeds. Austral Ecol. 13, 137–145.

Winn, A.A., 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. J. Ecol. 73, 831–840.

Zipparro, V.B., Morellato, L.P.C., 2005. Seed predation of *Virola bicuhyba* (Schott) Warb. (Myristicaceae) in the Atlantic forest of south-eastern Brazil. Rev. Bras. Bot. 28, 515–522.