

Seedling Community in a Patchy Tropical Vegetation Under the Influence of Bamboos

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Abstract

As a group adapted to invade disturbed sites, bamboos can dominate extensive areas and, thus, alter vegetation structure and dynamics. However, the effect of bamboo expansion associated to human activity on seedling communities in tropical forests remains poorly known. We investigated the correlation of the native bamboo *Guadua tagoara* presence for a year on the abundance, richness, diversity, dominance, evenness, emergence, mortality, and growth of the first months of the native seedlings establishment in an Atlantic forest area, São Paulo State, Brazil. Bamboo presence favored the initial establishment of the palm *Euterpe edulis* seedlings but altered seedling community structure as a whole. Species richness did not differ between bamboo and nonbamboo dominated habitats, but abundance, diversity, and evenness did. Bamboo habitats showed higher seedling abundance, emergence, and mortality than in habitats without bamboos. However, diversity was lower in these habitats. Our results shed light on the role of bamboo presence in limiting early establishment of native seedlings but favoring the first months of establishment of *E. edulis*, the dominant species in bamboo habitats (70%). Therefore, the monitoring of more specific variables could be included (i.e., bamboo culm density, soil type, decomposition of organic matter, fauna living, or foraging in bamboos) in future studies to better understand the consequences of bamboo dominance on the recruitment and dynamics of tropical forests biodiversity in the long term.

Keywords

assembly rules, ecological filters, invasive native bamboos, seedling recruitment

Introduction

Post-disturbances conditions favor many heliophyte species, such as lianas (César, Rother, & Brancalion, 2017; Schnitzer, Heijden, Mascaro, & Carson, 2014; Tabanez & Viana, 2000) and some bamboos (Burman & Filgueiras, 1993; Judziewicz, Clark, Londoño, & Stern, 1999). Lianas and bamboos are nontree life forms with high vegetative growth potential that may vigorously establish and grow in high densities after disturbances, altering forest structure on the long term (Burman & Filgueiras, 1993; Farah et al., 2014; Schnitzer, Dalling, & Carson, 2000).

Bamboo expansion is a typical example of local biological invasion caused by the interaction among the bamboo's aggressive monopolization of above- and belowground resources and disturbances created by humans or natural causes (e.g., harvesting, wind, tree fall, snow; see Yang et al., 2015). Characteristics such as morphology, high seed production, growth rate, and

clonal reproduction are important traits probably related to their ecological success and spread (Lima, Rother, Muler, Lepsch, & Rodrigues, 2012). Due to its

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dominance, some bamboo species can play a major role in forest dynamics, as they can alter population dynamic and the structure of the invaded community (Okutomi, Shinoda, & Fukuda, 1996; Veblen, 1982).

A series of studies from tropical and temperate forests have tried to understand the mechanisms behind bamboo dominance such as the disruption of ecological, functional, and structural processes, as well as other processes that shape ecosystem composition and biodiversity (Abe, Miguchi, & Nakashizuka, 2001; Giordano, Sánchez, & Austin, 2009; Muler et al., 2014; Peters, Nakashizuka, & Ohkubo, 1992; Rother, Rodrigues, & Pizo, 2009; Rother, Jordano, Rodrigues, & Pizo, 2013; Rother, Rodrigues, & Pizo, 2016; Taylor, Jinyan, & Shiqiang, 2004; Tripathi et al., 2005; Yang et al., 2015). Bamboos alter the vegetation structure by damaging both tall trees and regenerating plants and by altering the forest microclimate and largely increasing the biomass of leaf litter (Araujo, 2008). They can also influence the vegetation by altering seed rain (Grombone-Guaratini, Alves, Vinha, & Franco, 2014; Rother et al., 2009) and seed germination (Giordano et al., 2009) and by affecting the regeneration of tree species (Caccia, Chaneton, & Kitzberger, 2009; Campanello, Gatti, Ares, Montti, & Goldstein, 2007; Fantini & Guries, 2007; Oliveira-Filho, Vilela, Gavilanes, & Carvalho, 1994; Rother, Jordano, et al., 2013; Widmer, 1988), tree growth (Oliveira-Filho et al., 1994), and forest succession (Griscom & Ashton, 2003; Muler et al., 2014; Rother et al., 2016). Other studies assessed the relationship between bamboos and the vegetation by monitoring survival and recruitment of plant species in habitats covered by bamboos (Guilherme, Oliveira-Filho, Appolinário, & Bearzoti, 2004; Lima et al., 2012; Rother, Jordano, et al., 2013; Sanquetta, Dalla Corte, Salzmänn, & Vulcanis, 2007).

Both abiotic and biotic are important factors influencing plant dynamic, and their importance on plant community may vary in forest understory dominated by bamboos (Abe et al., 2001; Caccia et al., 2009; Lima et al., 2012). Lima et al. (2012) showed that bamboo-dominated habitats in Brazilian Atlantic forest have lower abundance of trees (>5 cm dbh), and they attribute that to physical-induced damages caused by *Guadua tagoara* loads on trees. There are evidences that bamboo effects on the early recruitment of tree species are patchy and species-specific (Rother, Jordano, et al., 2013). In a manipulating experiment, Rother, Jordano, et al. (2013) demonstrated that three tree species are especially susceptible to removal by rodents in the early establishment, and the mortality of seeds and seedlings can be more crucial than bamboo and nonbamboo differences as determinants of survival. It is interesting to note that some tree species find bamboo habitats as safe sites to survive successfully in the early establishment with potential implications for forest dynamics,

biodiversity, and succession (Caccia et al., 2009; Rother, Jordano, et al., 2013). This is also especially true to the occurrence of bamboo specialists' birds and birds that do not depend on forested habitats in bamboo areas (Rother, Alves, & Pizo, 2013).

The community seedling composition will depend on the specie-specific requirements and tolerances to various stress factors (Caccia et al., 2009). Light availability and quality are important factors to shape regeneration niches by defining seed germination, seedling emergence, and growth of understory species (Caccia et al., 2009). Authors found that canopy of bamboo-dominated habitats were more open than nonbamboo habitats. Studies also developed in Atlantic forest mention that at bamboo-dominated habitats, the vegetation has discontinuous canopy, low density of large and small trees, and low plant diversity (Fantini & Guries, 2007; Guilherme et al., 2004; Oliveira-Filho et al., 1994; Tabarelli & Mantovani, 1999).

Despite some studies carried out in the past decades, our knowledge of bamboos and their relationship with forest structure and dynamics remains incipient. In general, studies evaluating bamboo ecology highlight this group as important elements acting in positive or negative ways on the forest dynamic. Most studies, however, recognize the need for additional studies on the life cycle, evolution, and ecology of bamboos in forests (Judziewicz et al., 1999). Aiming at filling this gap, we assessed how the *G. tagoara* presence influences the structure and dynamic of the early stages of recruitment of native seedlings in an area of dense Atlantic forest. The expansion of this bamboo species in the Atlantic forest is mentioned as caused by the illegal extraction of palm heart (*Euterpe edulis*) (Fantini & Guries, 2007). Considering that the understory of *G. tagoara*-dominated forest has higher light incidence, thicker leaf litter (Rother et al., 2016), and higher mortality of native juvenile plants (Lima et al., 2012), we expected to find lower seedling abundance, richness, and growth in these areas than in bamboo-free forest.

Method

Study Area

Our study was carried out in Carlos Botelho state park at ca. 300 m a.s.l., on the Atlantic slope of the Paranapiacaba mountain range, in a 320 × 320 m (10.24 ha) permanent plot (24°10'S and 47°56'W), at São Paulo state, Brazil. The site is characterized by trees of 20 to 30 m height, the dominant palm *E. edulis* (jussara), scandent bamboos (*G. tagoara*), and species of the families Cyatheaceae, Rubiaceae, and Rutaceae in the understory (Custódio-Filho, 2002; Lima et al., 2011; Rizzini, 1979; Toniato et al., 2011). The bamboo *G. tagoara* covers about 3 ha of the total area of the

permanent plot, forming clumps throughout the plot that can range from 400 m² to 2,000 m² (Rother, Jordano, et al., 2013). These bamboo-dominated sites are interspersed with areas lacking bamboos forming a forest mosaic throughout the permanent plot (Rother, Jordano, et al., 2013). *Guadua* is the bamboo genus with the broadest distribution in America, comprising approximately 30 species (Londoño, 1998; Young & Judd, 1992). *G. tagoara* is a perennial bamboo with rhizomes, woody culms, 8 to 15 m height, 5 to 10 cm in diameter, erect at the base and leaning or scandent at the apex, with spinescent nodes with more developed thorns on the lower nodes, hollow internodes, deciduous stem leaves, sometimes persistent in basal nodes. *G. tagoara* stands are extremely patchy and dynamic, and its dominance is related to the anthropogenic (e.g., illegal *E. edulis* harvesting at the study site) or natural disturbances (e.g., gaps, landslides) (Lima et al., 2012). They promote a structural patchiness in the forest by altering the conditions (e.g., light availability, litter depth) for early recruitment of other plant species (Rother, Jordano, et al., 2013, 2016). Also, edges of bamboo patches are dynamic by advancing and retracting, changing consequently the forest structure. The mean temperature in the study period was 21.1°C (range, 17.4–25.2°C), and the site received 3,384 mm of rainfall. The rainiest and hottest season occurs from December to March. The soil developed over granites and colluvionar deposits and was classified as Haplic Cambisols and Fluvisols/Leptosols (Rodrigues, 2005).

Data Collection

We set up 80, 1 × 1 m plots for seedlings within the permanent plot in September 2004 being 40 in habitats with bamboos (B) and 40 in habitats without bamboos (NB). Plot location was randomized, but due to the slope of the area, some points needed reallocation, always maintaining a minimum of 20-m distance among each other. We marked all woody and herbaceous plants smaller than 30 cm in height (considered as seedlings) with plastic tags. Seedlings were numbered, and whenever possible, identified to the species level. Monthly during a year, we marked new individual plants which allowed to monitor the emergency and mortality. We did not sample individuals that showed vegetative growth or *stolon* due to the difficulty in defining their development stage (i.e., seedling or juvenile). For herbaceous plants, we considered as seedlings the individuals that did not show flowers or fruits during the study period. They were included in the abundance and diversity analysis. Due to their short life cycle compared to other life forms, they were not included in the analysis involving temporal dynamic, such as seedling emergence, mortality, and growth. We measured seedling height and diameter with a tape. Height was measured

from ground level to the apical meristem, and the diameter was taken at ground level. The height and diameter measurements were taken in September 2004, January 2005, and June 2005.

We identified seedlings by comparison with specimens from the HRCB Herbarium of the State University of Rio Claro and the University of São Paulo at Piracicaba, plants cultivated in the greenhouse of the Experimental Garden of the State University of Rio Claro, and by consulting the literature and specialists. Taxonomic nomenclature follows Angiosperm Phylogeny Group III (2009).

Data Analysis

To assess the effect of bamboo presence on the early seedling establishment, we considered two components: species composition and the abundance of seedlings sampled for each species. We calculated richness (S = number of species in the sample), Shannon–Wiener diversity index (H'), dominance (1-Simpson index), and Pielou evenness (J) (Magurran, 2013). These descriptors were calculated in the program Past 2.17c (Hammer, Harper, & Ryan, 2001) and compared between habitats with t tests. We used species accumulation curves and the bootstrap richness estimator to test for sampling completeness in B and NB habitats (Hortal, Borges, & Gaspar, 2006). Our objective was to estimate how many species were expected in a random seedling sample in both habitats. To perform this analysis, we used the *specpool* function in the package *vegan* for R 3.4.2 (R Development Core Team, 2017), which estimates the species richness extrapolated from a species pool (e.g., all species available that could potentially colonize and inhabit a determined area), or the number of not observed species.

Monthly data for seedling emergence and mortality between habitats were analyzed using a generalized linear mixed model, considering the habitat effect (B and NB) and a Poisson error distribution. Then, we modeled the relative growing rate (stem height recorded in Time 2 minus stem height recorded in Time 1 divided by the stem height recorded in Time 1, expressed in percentage) as a function of the habitats using a linear mixed model. The relative growth was used to eliminate the effect due to different seedling sizes. In all the mixed models, the random effect was defined as 1 × 1 plots and fixed effect as habitat (B and NB). The habitat influence over emergence and mortality was tested through the coefficient significance during generalized linear mixed model adjust assessed by a z test (Bates, Maechler, Bolker, & Walker, 2015). The relative growth of all seedlings was compared to *E. edulis* by an analysis of variance between mixed models, considering the likelihood ratio test proposed by Pinheiro and Bates (Bolker et al., 2009). We performed that analysis due to the dominance of *E. edulis* seedlings in the plots. We used the

packages *stats*, *lme4*, *sandwich*, and *lme4*, for R 3.4.2 (R Development Core Team, 2017).

Results

Seedling Abundance and Diversity

We recorded a total of 982 seedlings. Of this total, 638 seedlings were recorded in B plots and 344 in NB plots. *E. edulis* was the most abundant species in both habitats. In B plots, we recorded 466 *E. edulis* seedlings, which represented 73% of the total of individuals sampled, followed by two undetermined species, and *Tetrastylidium grandifolium* (Olacaceae). In NB plots, we sampled 82 individuals of that species, which represented 23% of the individuals sampled, followed by one undetermined species, *Rudgea jasminoides* (Rubiaceae) and *Eugenia mosenii* (Myrtaceae) (see Appendix A for seedling species recorded in both habitats).

Table 1. Richness, Abundance, Dominance, Diversity Index (Shannon, H'), and Evenness (Pielou, J) for Bamboo and Nonbamboo Habitats in the Permanent Plot Located in Carlos Botelho State Park, State of São Paulo, Southeastern Brazil.

	Bamboo	Nonbamboo	p
Richness	70	60	.914
Individuals	638	344	.000
Dominance	0.54	0.11	.001
Shannon H'	1.49	2.90	.001
Evenness J	0.35	0.71	.001

Note. p values represent the comparison between habitats.

We found a total of 104 seedling species being 70 in B plots and 60 in NB plots, and seedling richness was similar between habitats ($p > .05$; Table 1). Among them, 44 species were exclusive to B plots, 34 were exclusive to NB plots, and 26 species (25%) were common to both habitats. There was lower species evenness in B plots. *E. edulis* was the most frequent and abundant species, which resulted in a lower diversity (Table 1). In NB plots, diversity was higher due to higher evenness, which differed significantly from that of B plots (Table 1).

Considering the estimation of how many species were expected in a random seedling sample in both habitats in B plots, seedling richness was estimated as 88.86 (± 5.43), whereas in NB plots, it was estimated as 74.55 (± 4.18 ; Table 1; Figure 1). Contrasting the observed and the extrapolated species richness, this result suggests that sampling of seedlings was relatively complete (Table 1; Figure 1), although the rarefaction curves did not reach an asymptote for either bamboo and nonbamboo plots (Figure 1).

Seedling Emergence, Mortality, and Growth

The emergence and mortality were affected by bamboo presence (emergence: $z = -2.756$, $p = .00584$; mortality: $z = -524$, $p = < 2e-16$). NB plots showed a lower seedling emergence and mortality (Figure 2). Emergence in NB was 0.66 seedlings per plot (± 0.24 standard error) lower than B plots, and mortality was about 0.46 seedlings per plot (± 0.001 standard error) lower than B plots. Bamboo presence did not affect the relative growth rate in seedlings height ($\chi = 0.34$, $p = .56$). Abundance of *E. edulis* seedlings in B plots was threefold higher than NB plots (Table 1); however, the relative growth rate of

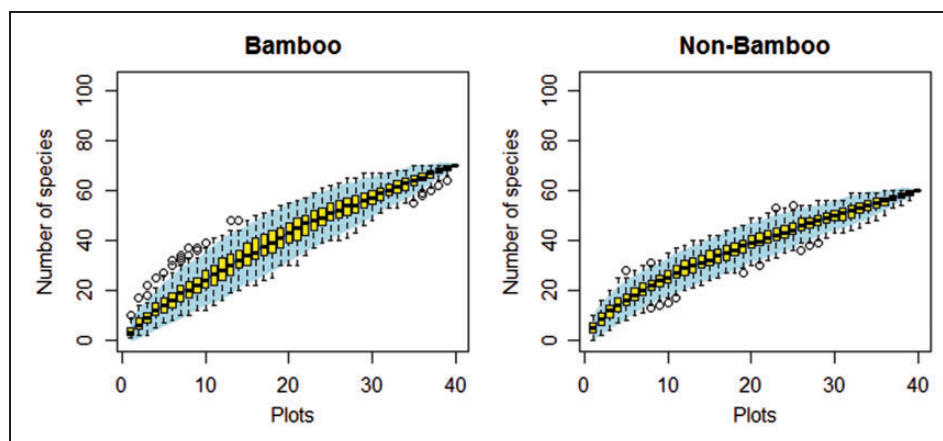


Figure 1. Rarefaction curves of the seedling species recorded in plots with bamboos (left) and without bamboos (right) in the permanent plot located in Carlos Botelho State Park, state of São Paulo, southeastern Brazil. The blue area represents the confidence interval for $N = 100$ permutations. Boxplots (yellow) represent the median, and 50%, 90%, and extreme values.

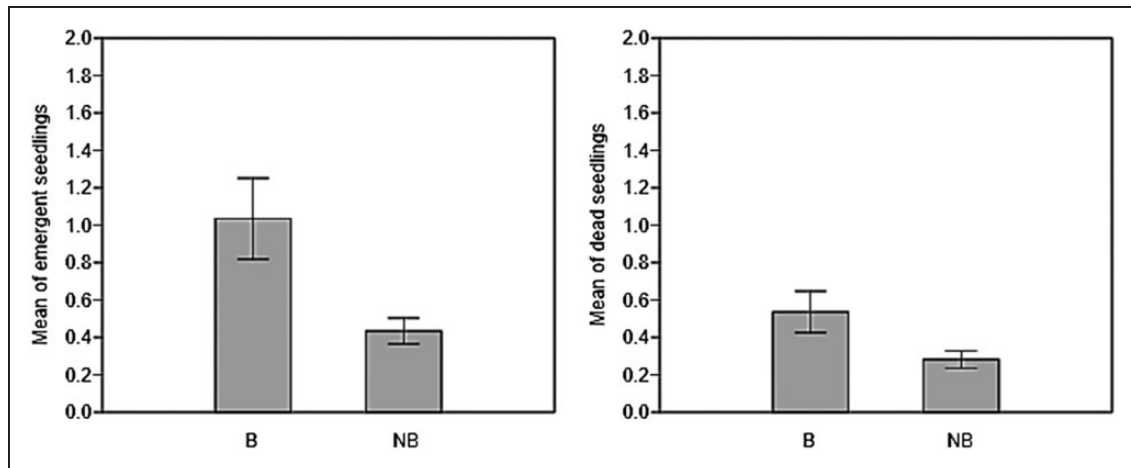


Figure 2. Boxplot comparing emergence and mortality (mean \pm SE) of seedlings between habitats (B = bamboo and NB = nonbamboo) in Carlos Botelho State Park, state of São Paulo, southeastern Brazil.

E. edulis seedlings was the same for both habitats ($\chi = 2.21$, $p = .14$).

Discussion

Bamboos affected the community structure and dynamics of the early seedling establishment in the study area. Seedling turnover (emergence and mortality) was higher in habitats with bamboos. In general, the closed canopy can increase seedling mortality by reducing light penetration in the floor (Camargo & Kapos, 1995); however, a previous study carried out in the same site demonstrated greater luminosity in the bamboo habitats (Rother et al., 2016). In contrast, studies on the influence of bamboo on forest succession in China (Taylor & Zisheng, 1988) and Japan (Tanaka, 1988) have attributed reduced seedling density to reduced levels of light under bamboos. Other studies have reported decreasing recruitment and mortality on the fall of canopy debris damaging seedlings (Benitez-Malvido, 1995; Clark & Clark, 1989, 1991; Lima et al., 2012), trampling by animals (Aizen & Feizinger, 1994), litter depth (Griscom & Ashton, 2003; Rother et al., 2016) or the attack of ants, Orthoptera (Alvarez-Buylla & Martínez-Ramos, 1990), and pathogens (Abe et al., 2001). Possibly some of these factors or their interactive effect may have resulted in higher seedling mortality in the bamboo habitats. On the other hand, the conditions for seedling emergence under bamboos seem to have been more favorable than those without bamboos. However, it is interesting to highlight that this result is closely related to the emergence of high number of *E. edulis* seedlings in bamboo habitats.

G. tagoara-dominated habitats revealed lower seedling diversity as denoted by the low evenness resulting mostly from the dominance of *E. edulis* seedlings. The decrease in seedling diversity, especially of tree species

(low abundance of seedlings excluding *E. edulis* 92 tree seedlings for NB and 56 tree seedlings for B), is the main problem in bamboo-dominated habitats, as trees correspond to the most important plant functional group for diversity, structure, and functioning of tropical forests (Denslow, 1987).

The illegal harvesting of adult *E. edulis* in the Atlantic forest results in changes in forest structure and local biotic characteristics (Rother et al., 2016). The gaps opened by the removal of palm trees are habitats with great light incidence, which favors the establishment and dominance of bamboos, but also favors the establishment of *E. edulis*, which forms a seedling bank under bamboo stands. As previously demonstrated, *E. edulis* is favored in its early life cycle stages in habitats with bamboos (Rother et al., 2016). Seedlings of this palm tree corresponded to over 70% of the seedling community in these habitats. This result seems interesting at first, as *E. edulis* is an endangered species due to the illegal exploitation of adult individuals for palm heart. However, the population structure of this palm species had higher mortality of juvenile individuals in habitats with bamboos (Rother et al., 2016). Although bamboo habitats have a positive effect on seedling recruitment of *E. edulis*, they arrest the later stages of the life cycle of this palm species probably due to physical damages on the juveniles (Rother et al., 2016). Therefore, bamboos represent a demographic bottleneck for *E. edulis*, thus changing its population structure.

Bamboo-dominated habitats have a different seedling community than that found in habitats without bamboos, the latter being composed by a smaller number of exclusive species. What we still do not know is how the seedling community maintains itself or changes in the long term. A past study pointed out that seed rain is not strongly affected by bamboos (Rother et al., 2009),

but they have a negative influence on the seedling density of some tree species (Rother, Jordano, et al., 2013). Habitats with bamboos show higher concentration of small trees (<5 cm dbh) (Lima et al., 2012), higher light incidence, and thicker leaf litter (Rother et al., 2016). Hence, evidence shows that the forest structure is strongly influenced by *G. tigoara*. The physical damage caused by the fall of culms on the plants and the physiological stress caused by high luminosity and temperature in habitats with bamboos probably make these habitats extremely dynamic (Lima et al., 2012). Although some bamboo-dominated sites may have a higher concentration of smaller trees as the studied site (Lima et al., 2012), this is not always the case. Griscom and Ashton (2003), for example, found that juveniles (5–29 cm dbh) were more severely damaged than mature trees in *Guadua*-dominated forests.

Contrary to what we expected, habitats with bamboos showed higher seedling abundance. Explanations based on niche processes depend on differences between species and the way they respond to the environment (Chesson, 2000; Tilman & Pacala, 1993). The higher light incidence in bamboo-dominated habitats (Rother et al., 2016) may have favored light-demanded species in their initial establishment, such as *E. edulis* (466 seedlings). Indeed, bamboo-dominated habitats receive higher density of *E. edulis* seeds than nonbamboo habitats (Rother et al., 2009), which could explain this great seedling density of this palm species. Authors attribute two main hypotheses to explain the seed density differences between habitats. Despite both habitats have similar densities of adults, at bamboo habitats, *E. edulis* adults are more exposed to light which may lead them to greater seed production, and also the fruits are more conspicuous to seed-eaten animals.

Basically, canopy species might function as diversity filters as they strongly influence the environment located under their crown (Souza, Gandolfi, & Rodrigues, 2014). Therefore, the canopy of trees or bamboos might affect light incidence in the understory and soil (Souza et al., 2014; Vázquez-Yanes & Orosco-Segovia, 1990; Vázquez-Yanes et al., 1990), soil surface temperature (Molofsky & Augspurger, 1992), seed germination, seedling recruitment, and the deposition and decomposition of leaf litter (Metcalfe & Turner, 1998; Ponge et al., 1998; Rother, Jordano, et al., 2013, 2016). Consequently, these variables have a different influence on species composition in different habitats, as they select seedlings of species that are better adapted to different microhabitat conditions. The outcomes of understory tree seedlings regarding the environment will depend on the species' requirements and tolerances to various abiotic and biotic factors (Abe et al., 2001). To demonstrate such differences in species performance, Rother, Jordano, et al. (2013) showed that the most favorable habitat for

seeds and seedlings of *E. edulis* and *Virola bicuhyba* were bamboo-dominated habitats, while they were the least favorable for *Sloanea guianensis*.

Species classification according to forest dynamics strategies is controversial in the literature, as plants are subjected to a complex set of variables (Oliveira-Filho et al., 1994). Under natural conditions, bamboos create different regeneration niches. However, the increase and superdominance of this group can have negative consequences on plant life cycles, as bamboos can limit seedling emergence and mortality. We observed that habitats with and without bamboos showed a tendency to select some species by limiting the establishment differently. Excluding *E. edulis* seedlings of the both habitats, we notice that the species composition and abundance are very different (Appendix A). Considering that the life cycle (average 7.4 years between flowering seasons, see Alves, 2007) and the structure of the *G. tigoara* environment are extremely dynamic, long-term studies are crucial to understand the effects of its dominance on late stages of plant recruitment, as well as on biodiversity dynamic, in tropical forests.

Implications for Conservation

Disturbances of tropical forest alters structure and ecological processes of the vegetation (César et al., 2017; Lima et al., 2012). Illegal harvests of palm heart create gaps that favor bamboo proliferation (Fantini & Guries, 2007). In the studied site, this activity benefits proliferation of *G. tigoara* that when overabundant, they may negatively affect important processes to forest regeneration. Factors appeared to be limited especially to physical damage, physiological stress by not only high light incidence and litter depth but also seed removal by rodents and mammal trampling on seedlings (Rother, Jordano, et al., 2013). We tested the prediction that *G. tigoara* presence influences the structure and dynamic of the community of the first months of establishment of the seedlings, a fundamental ecological process to forest dynamic. We found that in bamboo habitats, the initial establishment of the palm *E. edulis* seedlings was favored, but the seedling community structure was altered as a whole. Also, we found that habitats with bamboos showed higher seedling abundance, emergence, and mortality than in habitats without bamboos. In a short term, we conclude that bamboo presence may limit the early establishment of native seedlings but favor *E. edulis* establishment. However, there is evidence that bamboos are functioning as a demographic bottleneck for later stages of *E. edulis* populations (Rother et al., 2016). Over time, the dominance of bamboos may have negative consequences in the future tree community, but this issue needs more investigation for long-term monitoring. Despite these evidences of negative influence of bamboos

on the forest regeneration, this bamboo species is an important element to the forest providing sources of food, perches, and shelter for bamboo specialist birds and birds not dependent on forested habitat (Rother, Alves, et al., 2013). Attempts to control this bamboo species remain premature (Lima et al., 2012) and need parsimony. Therefore, it is essential to test different experimental methods to manage *G. tagoara* and to monitor variables such as fauna populations, cover, litter, and ecological processes after management.

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References

- Abe, M., Miguchi, H., & Nakashizuka, T. (2001). An interactive effect of simultaneous death of dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. *Oecologia*, 127(2): 281–286. doi:10.1007/s004420000585.
- Aizen, M., & Feinsinger, P. (1994). Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, 75(2): 330–351. doi:10.2307/1939538.
- Alvarez-Buylla, E. R., & Martínez-Ramos, M. (1990). Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia*, 84(3): 314–325. doi:10.1007/BF00329755.
- Alves, G. T. R. (2007). *Aspectos da história de vida de Guadua tagoara* (Nees) Kunth (Poaceae: Bambuseae) na Serra dos Órgãos, RJ [Aspects of the life history of *Guadua tagoara* (Nees) Kunth (Poaceae: Bambuseae) in Serra dos Órgãos, RJ] (Dissertation). Universidade Federal de São Carlos, São Carlos, Brazil.
- Angiosperm Phylogeny Group III. (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, 161, 105–121. doi:10.1111/j.1095-8339.2009.00996.x.
- Araujo, L. S. (2008). *Padrões e condicionantes da dinâmica da paisagem na floresta com bambus do Parque Estadual Intervales, SP* [Patterns and conditioners of the landscape dynamics in the bamboo forest of the Intervales State Park, SP] (PhD in Forest Resources). Escola Superior de Agricultura Luiz de Queiroz, USP, Piracicaba. doi:10.11606/T.91.2008.tde-25072008-105206.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1): 1–48. doi:10.18637/jss.v067.i01.
- Benitez-Malvido, J. (1995). *The ecology of seedlings in central Amazonian forest fragments* (PhD Dissertation). UK: University of Cambridge.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24(3): 127–135. doi:10.1016/j.tree.2008.10.008.
- Burman, A. G., & Filgueiras, T. S. (1993). A review of the woody bamboo genera of Brazil (Gramineae: Bambusoideae: Bambuseae). *Thaiszia*, 3, 53–88. doi:10.11646/phytotaxa.267.3.5.
- Camargo, J. L., & Kapos, V. (1995). Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, 11(2): 205–221. doi:10.1017/S026646740000866X.
- Campanello, P. I., Gatti, M. G., Ares, A., Montti, L., & Goldstein, G. (2007). Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *Forest Ecology and Management*, 252, 108–117. doi:10.1016/j.foreco.2007.06.032.
- Caccia, F. D., Chaneton, E. J., & Kitzberger, T. (2009). Direct and indirect effects of understorey bamboo shape tree regeneration niches in a mixed temperate forest. *Oecologia*, 161, 771–780. doi:10.1007/s00442-009-1412-z.
- César, R. G., Rother, D. C., & Brancalion, P. H. S. (2017). Early response of tree seed arrival after liana cutting in a disturbed tropical forest. *Tropical Conservation Science*, 10, 1–7. doi:10.1177/1940082917723586journals.sagepub.com/home/trc.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology, Evolution and Systematics*, 31, 343–366. doi:10.1146/annurev.ecolsys.31.1.343.
- Clark, D. B., & Clark, D. A. (1989). The role of physical damage in the seedlings mortality regime of a neotropical rain forest. *Oikos*, 55(2): 225–230. Retrieved from <http://www.jstor.org/stable/3565426>.
- Clark, D. B., & Clark, D. A. (1991). The impact of physical damage on canopy tree regeneration in a tropical rain forest. *Journal of Ecology*, 79(2): 447–457.
- Custódio-Filho, A. (2002). *A Floresta Ombrófila Densa em diferentes altitudes no Parque Estadual Carlos Botelho, São Paulo, Brasil* [The dense ombrophilous forest at different altitudes in Carlos Botelho State Park, São Paulo, Brazil] (PhD in Sciences). Instituto de Biociências, Universidade de São Paulo, São Paulo.
- Denslow, J. S. (1987). Tropical rain-forest gaps and tree species-diversity. *Annual Review of Ecology, Evolution and Systematics*, 18, 431–451. doi:10.1146/annurev.es.18.110187.002243.
- Fantini, A. C., & Guries, R. P. (2007). Forest structure and productivity of palmito (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. *Forest Ecology and Management*, 242, 185–194. doi:10.1016/j.foreco.2007.01.005.

- Farah, F. T., Rodrigues, R. R., Santos, F. A. M., Tamashiro, J. Y., Shepherd, G. J., Siqueira, T., Batista, J. L. F., & Manly, B. J. F. (2014). Forest destructuring as revealed by the temporal dynamics of fundamental species – Case study of Santa Genebra Forest in Brazil. *Ecological Indicators*, 37, 40–44. doi:10.1016/j.ecolind.2013.09.011.
- Giordano, C. V., Sánchez, R. A., Austin, A. T., & Austin, A. T. (2009). Gregarious bamboo flowering opens a window of opportunity for regeneration in a temperate forest of Patagonia. *New Phytologist*, 181, 880–889.
- Griscom, B. W., & Ashton, P. M. S. (2003). Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. *Forest Ecology and Management*, 175, 445–454. doi:10.1016/S0378-1127(02)00214-1.
- Grombone-Guaratini, M. T., Alves, L. F., Vinha, D., & Franco, G. A. D. (2014). Seed rain in areas with and without bamboo dominance within an urban fragment of the Atlantic Forest. *Acta Botanica Brasílica*, 28, 76–85. doi:10.1590/S0102-33062014000100008.
- Guilherme, F. A. G., Oliveira-Filho, A. T., Appolinário, 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 Ecology*, 174, 19–36. doi:10.1023/B:VEGE.0000046051.97752.cd.
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electronica*, 4(1): 1–9.
- Hortal, J., Borges, P., & Gaspar, C. (2006). Evaluating the performance of species richness estimators: Sensitivity to sample grain size. *Journal of Animal Ecology*, 75, 274–287. doi:10.1111/j.1365-2656.2006.01048.x.
- Judziwicz, E. J., Clark, L. G., Londoño, X., & Stern, M. J. (1999). *American bamboos*. Washington, DC: Smithsonian Institution.
- 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, Brazil [Vascular flora of the Carlos Botelho State Park, São Paulo, Brazil]. *Biota Neotropica*, 11(4): 173–214. doi:10.1590/S1676-06032011000400018.
- Lima, R. A. F., Rother, D. C., Muler, A. E., Lepsch, I. F., & Rodrigues, R. R. (2012). Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot. *Biological Conservation*, 147, 32–39. doi:10.1016/j.biocon.2012.01.015.
- Londoño, X. (1998). A decade of observations of a *Guadua angustifolia* plantation in Colombia. *Journal of American Bamboo Society*, 12, 37–43.
- Magurran, A. E. (2013). *Medindo a diversidade biológica [Measuring biological diversity]*. Curitiba, Brazil: Editora da UFPR.
- Metcalf, D. J., & Turner, I. M. (1998). Soil seed bank from lowland rain forest in Singapore: Canopy-gap and litter-gap demands. *Journal of Tropical Ecology*, 14, 103–108. doi:10.1017/S0266467498000091.
- Molofsky, J., & Augspurger, C. K. (1992). The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology*, 73, 68–77. doi:10.2307/1938721.
- Muler, A., Rother, D. C., Brancalion, P. H. S., Naves, R. P., Rodrigues, R. R., & Pizo, M. A. (2014). Can overharvesting of a non-timber-forest product change the regeneration dynamics of a tropical rainforest? The case study of *Euterpe edulis*. *Forest Ecology and Management*, 324, 117–125. doi:10.1016/j.foreco.2013.09.001.
- Okutomi, K., Shinoda, S., & Fukuda, H. (1996). Causal analysis of the invasion of broadleaved forest by bamboo in Japan. *Journal of Vegetation Science*, 7, 723–728. doi:10.2307/3236383.
- Oliveira-Filho, A. T., Vilela, E. A., Gavilanes, M. L., & Carvalho, D. A. (1994). Effect of flooding regime and understorey bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in southeastern Brazil. *Vegetatio*, 113, 99–124. doi:10.1007/BF00044229.
- Peters, R., Nakashizuka, T., & Ohkubo, T. (1992). Regeneration and development in beech dwarf bamboo forest in Japan. *Forest Ecology Management*, 55, 35–50. doi:10.1016/0378-1127(92)90090-V.
- Ponge, J. F., André, J., Zackrisson, O., Bernier, N., Nilsson, M. C., & Gallet, C. (1998). The forest regeneration puzzle. *BioScience*, 48(7): 523–530. doi:10.2307/1313314.
- R Development Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <http://www.R-project.org/>.
- Rizzini, C. T. (1979). *Tratado de fitogeografia do Brasil: Aspectos sociológicos e florísticos* [Treaty of phytogeography of Brazil: Sociological and floristic aspects]. São Paulo, Brazil: Hucitec/EdUSP.
- Rodrigues, R. R. (Coord.) (2005). Parcelas Permanentes em 40 ha de florestas do Estado de São Paulo: Uma experiência interdisciplinar. 40 Relatório temático do projeto “Diversidade, dinâmica e conservação em florestas do estado de São Paulo: 40,96 há de parcelas permanentes” apresentado à FAPESP (Processo nº: 1999/09635-0). Piracicaba, Brazil: ESALQ/USP, Departamento de Ciências Biológicas. Retrieved from <http://www.lerf.esalq.usp.br/parrel2005.php>.
- Rother, D. C., Alves, K. J. F., & Pizo, M. A. (2013). Avian assemblages in bamboo and non-bamboo habitats in a tropical rainforest. *Emu*, 113, 52–61. doi:10.1071/MU12017.
- Rother, D. C., Jordano, P., Rodrigues, R. R., & Pizo, M. A. (2013). Demographic bottlenecks in tropical plant regeneration: A comparative analysis of causal influences. *Perspectives in Plant Biology, Systematics and Evolution*, 15, 86–96. doi:10.1016/j.ppees.2012.12.004.
- Rother, D. C., Rodrigues, R. R., & Pizo, M. A. (2009). Effects of bamboo stands on seed rain and seed limitation in a rainforest. *Forest Ecology and Management*, 257, 885–892. doi:10.1016/j.foreco.2008.10.022.
- Rother, D. C., Rodrigues, R. R., & Pizo, M. A. (2016). Bamboo tickets alter the structure of *Euterpe edulis* population: A threatened palm of the Atlantic forest. *Acta Oecologica*, 70, 96–102. doi:10.1016/j.actao.2015.11.008.
- Sanquetta, C. R., Dalla Corte, A. P., Salzmann, A. M., & Vulcanis, L. (2007). Dinâmica de um remanescente de Floresta Ombrófila Mista no sul do Paraná sob influência de taquaras [Dynamics of a remnant of Mixed Ombrophylous Forest in southern Paraná under the influence of taquaras]. *Ambiência*, 3, 65–78.
- Schnitzer, S. A., Dalling, J. W., & Carson, W. P. (2000). The impact of lianas on tree regeneration in canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, 88, 655–666. doi:10.1046/j.1365-2745.2000.00489.x.

- Schnitzer, S. A., Heijden, G., Mascaro, J., & Carson, W. P. (2014). Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology*, 95, 3008–3017. doi:10.1890/13-1718.1.
- Souza, F. M., Gandolfi, S., & Rodrigues, R. R. (2014). Deciduousness influences the understory community in a semi-deciduous tropical forest. *Biotropica*, 46, 512–515. doi:10.1111/btp.12137.
- Tabanez, A. A. J., & Viana, V. M. (2000). Patch structure within Brazilian Atlantic Forest fragments and implications for conservation. *Biotropica*, 32, 925–933. doi:10.1646/0006-3606(2000)032[0925:PSWBAF]2.0.CO;2.
- Tabarelli, M., & Mantovani, W. (1999). A regeneração de uma floresta tropical montana após corte e queima (São Paulo-Brasil) [Regeneration of a tropical montane forest after cutting and burning (São Paulo – Brazil)]. *Revista Brasileira de Biologia*, 59(2): 239–250.
- Tanaka, N. (1988). Tree invasion into patchy dwarf-bamboo thickets within a climax beech-fir forest in Japan. In: J. J. Dunning, M. J. A. Werger, & J. H. Willems (Eds). *Diversity and pattern in plant communities*. The Hague, Netherlands: Academic Publishing.
- Taylor, A. H., & Zisheng, Q. (1988). Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong natural reserve, Sichuan, China. *Journal of Ecology*, 76(4): 1204–1218.
- Taylor, A. H., Jinyan, H., & Shiqiang, Z. (2004). Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies-Betula* forests in southwestern China: A 12-year study. *Forest Ecology and Management*, 200, 347–360. doi:10.1016/j.foreco.2004.07.007.
- Tilman, D., & Pacala, S. (1993). The maintenance of species richness in plant communities. In: R. E. Ricklefs, & D. Schuler (Eds). *Species diversity in ecological communities* (pp. 13–25). Chicago, IL: Chicago Press.
- Toniato, M. T. Z., Ivanauskas, N. M., Souza, F. M., Mattos, I. F. A., Baitello, J. B., Kanashiro, M. M., ... Dittrich, V. A. O. (2011). A vegetação do Parque Estadual Carlos Botelho: Subsídios para o Plano de Manejo [The vegetation of Carlos Botelho State Park: Subsidies for the Management Plan]. *IF Serie Registros*, 43, 1–254.
- Tripathi, S. K., Sumida, A., Shibata, H., Uemura, S., Ono, K., & Hara, T. (2005). Growth and substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii* forest of northern Japan: Effects of the removal of understory dwarf bamboo (*Sasa kurilensis*). *Forest Ecology and Management*, 212, 278–290. doi:10.1016/j.foreco.2005.03.030.
- Vázquez-Yanes, C., & Orozco-Segovia, A. (1990). Ecological significance of light controlled seed germination in two contrasting tropical habitats. *Oecologia*, 83, 171–175. doi:10.1007/BF00317748.
- Vázquez-Yanes, C., Orozco-Segovia, A., Rincón, E., Sánchez-Coronado, M. E., Huante, P., Toledo, J. R., & Barradas, V. L. (1990). Light beneath the litter in a tropical forest: Effect on seed germination. *Ecology*, 71(5): 1952–1958. doi:10.2307/1937603.
- Veblen, T. T. (1982). Growth pattern of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bulletin of the Torrey Botanical Club*, 109(4): 474–487. doi:10.2307/2996488.
- Widmer, Y. (1998). Pattern and performance of understorey bamboos (*Chusquea* spp) under different canopy closures in old-growth oak forests in Costa Rica. *Biotropica*, 30(3): 400–415. doi:10.1111/j.1744-7429.1998.tb00074.x.
- Yang, Q. P., Yang, G. Y., Song, Q. N., Shi, J. M., Ouyang, M., Qi, H. Y., Qi, & Fang, X. M. (2015). Ecological studies on bamboo expansion: Process, consequence and mechanism. *Chinese Journal of Plant Ecology*, 39(1): 110–124. doi:10.17521/cjpe.2015.0012.
- Young, S. M., & Judd, W. S. (1992). Systematics of the *Guadua angustifolia* complex (Poaceae: Bambusoideae). *Annals of the Missouri Botanical Garden*, 79(4): 737–769. doi:10.2307/2399719.

Appendix A

Seedling Species Recorded at Bamboo and Nonbamboo Habitats in the Permanent Plot Located in Carlos Botelho State Park, State of São Paulo, Southeastern Brazil.

Seedling species	Bamboo	Nonbamboo
<i>Abuta selloana</i>	0	3
Araliaceae l	1	0
<i>Ardisia martiana</i>	0	1
<i>Bauhinia guianensis</i>	0	1
<i>Byrsonima</i> sp.	1	0
<i>Casearia decandra</i>	1	3
<i>Casearia</i> sp.	0	1
<i>Casearia</i> sp. 1	1	0
<i>Casearia</i> sp. 2	2	7
<i>Casearia sylvestris</i>	1	1
<i>Cecropia glaziovii</i>	4	0
<i>Chrysophyllum viride</i>	0	11
<i>Coccosyrselum lanceolatum</i>	1	0
<i>Copaifera trapezifolia</i>	1	0
<i>Cordia</i> sp.	3	0
<i>Cryptocarya moschata</i>	1	1
<i>Cupania</i> sp.	1	0
<i>Dorstenia hirta</i>	0	1
<i>Eugenia cuprea</i>	2	0
<i>Eugenia melanogyna</i>	4	1
<i>Eugenia mosenii</i>	0	23
<i>Eugenia oblongata</i>	1	0
<i>Eugenia</i> sp. 1	1	1
<i>Eugenia</i> sp. 2	0	2
<i>Euphorbiaceae</i> l	1	0
<i>Euterpe edulis</i>	466	82
<i>Geonoma</i> sp.	5	10
<i>Gomidesia</i> sp.	1	1
<i>Gomidesia spectabilis</i>	1	2

(continued)

Continued.			Continued.		
Seedling species	Bamboo	Nonbamboo	Seedling species	Bamboo	Nonbamboo
<i>Guapira opposita</i>	3	0	Rubiaceae 2	2	3
<i>Hymenaea courbaril</i>	1	0	Rubiaceae 5	0	1
<i>Inga edulis</i>	1	0	Rubiaceae 6	1	0
<i>Inga marginata</i>	2	2	<i>Rudgea jasminoides</i>	3	23
<i>Inga sessilis</i>	0	1	Sapindaceae 1	2	1
<i>Inga</i> sp.	1	1	<i>Sapium glandulatum</i>	1	0
<i>Inga</i> sp. 3	1	0	<i>Sloanea</i> sp.	0	2
<i>Inga</i> sp. 4	1	0	<i>Strychnos brasiliensis</i>	1	0
<i>Ixora</i> sp.	0	1	<i>Tetrastylidium grandifolium</i>	6	20
<i>Leandra mosenii</i>	1	0	Undetermined 1	5	6
<i>Mikania</i> sp.	3	0	Undetermined 10	1	0
<i>Mollinedia schottiana</i>	1	0	Undetermined 11	0	1
<i>Mollinedia</i> sp.	1	0	Undetermined 12	0	1
<i>Monstera adansonii</i>	1	0	Undetermined 13	0	1
<i>Myrsine hermogenesii</i>	3	7	Undetermined 14	1	0
Myrtaceae 1	1	3	Undetermined 15	1	0
Myrtaceae 10	0	1	Undetermined 18	0	1
Myrtaceae 2	0	1	Undetermined 2	1	1
Myrtaceae 4	1	0	Undetermined 20	0	1
Myrtaceae 5	1	0	Undetermined 21	0	1
Myrtaceae 6	1	0	Undetermined 22	1	0
Myrtaceae 7	1	0	Undetermined 23	1	0
Myrtaceae 8	0	1	Undetermined 24	0	1
Myrtaceae 9	1	0	Undetermined 25	3	1
<i>Nectandra</i> sp.	2	0	Undetermined 26	3	13
<i>Neomitranthes glomerata</i>	0	6	Undetermined 27	52	67
<i>Parinari excelsa</i>	1	0	Undetermined 28	0	1
<i>Paullinia trigonia</i>	0	3	Undetermined 29	1	0
<i>Philodendron</i> sp.	1	0	Undetermined 30	0	1
Piperaceae 1	1	3	Undetermined 31	9	0
Piperaceae 2	0	2	Undetermined 5	1	0
<i>Posoqueria acutifolia</i>	0	2	Undetermined 6	1	0
<i>Pouteria</i> sp.	0	1	Undetermined 7	0	2
<i>Protium widgrenii</i>	1	0	Undetermined 9	1	0
<i>Psychotria</i> cf. <i>leiocarpa</i>	0	1	<i>Virola bicuhyba</i>	5	1
<i>Psychotria</i> sp.	2	3	<i>Zanthoxylum rhoifolium</i>	0	1
<i>Psychotria</i> sp. 2	1	0			
<i>Psychotria umbellata</i>	0	1			
Rubiaceae 1	0	1			

(continued)