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# Maranthaceae overabundance decreases richness and abundance of regenerating woody plants in natural gaps

## A superabundância de Maranthaceae reduz a riqueza e abundância de espécies arbustivo-arbóreas em regeneração em clareiras naturais

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## Abstract

Natural gaps are known to be one of the most common disturbance types in tropical forests. Maranthaceae is one of the most important herb families and some studies on gaps address the influence of herbs on the regeneration of shrubs and trees. Maranthaceae are common and sometimes dominant herbs in tropical forest gaps. In this study we investigated the impact of Maranthaceae overabundance on the regeneration of woody species in natural gaps in a bamboo-dominated (*Guadua weberbaueri* Pilg.; Poaceae) forest fragment in southwestern Amazonia. We sampled 20 natural gaps, where Maranthaceae and woody plants with height ≥ 1 m and DBH ≤ 10 cm were counted, measured and identified. We used NMDS for species composition analyses and a GLM to test the influence of Maranthaceae overabundance on woody species richness and abundance. We also measured the similarity of woody species richness and abundance among Maranthaceae dominated and non-dominated gaps. The NMDS shows a distinction between Maranthaceae dominated and non-dominated gaps. The overabundance of Maranthaceae reduced significantly the richness and abundance of woody species. Species composition was also dissimilar among gaps and was influenced by Maranthaceae overabundance.

**Keywords:** natural disturbances, herbaceous, plant succession.

## Resumo

Clareiras naturais são um dos tipos de distúrbios mais estudados em florestas tropicais. Maranthaceae é uma das famílias mais importantes de ervas terrestres e alguns estudos têm mostrado a dominância de espécies dessa família em relação a outras espécies herbáceas em clareiras naturais. Nesse contexto, o objetivo deste trabalho foi verificar se existe influência da superabundância de Maranthaceae sobre a regeneração de espécies arbustivo-arbóreas em clareiras naturais em um remanescente de floresta aberta dominada por bambu (*Guadua weberbaueri* Pilg.; Poaceae) no sudoeste da Amazônia. Foi amostrada a regeneração ≥ 1 cm de diâmetro e os indivíduos de Maranthaceae em 20 clareiras formadas pela queda de árvores do dossel. Foi realizada uma análise não métrica de escalas multidimensionais (NMDS) para análise de composição de espécies e foram aplicados modelos lineares generalizados (GLM) para testar o efeito da superabundância de Maranthaceae sobre a riqueza e abundância de árvores e arbustos e da similaridade entre as clareiras dominadas e não dominados por essas herbáceas. A NMDS realizada mostrou separação das clareiras que foram dominadas por indivíduos de Maranthaceae daquelas não dominadas. A superabundância de Maranthaceae reduziu significativamente a abundância e riqueza de espécies e tornou os ambientes dominados dissimilares em termos de composição de espécies.

**Palavras-chave:** distúrbios naturais, herbáceas, sucessão vegetal.

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## Introduction

The mechanisms that maintain high tree diversity in tropical forests have long drawn the interest of ecologists. The study of these mechanisms led to the formulation of several hypotheses aimed at explaining the coexistence of a large number of species in a small area (Connell, 1978; Denslow, 1980; Hubbell *et al*., 1999; Wright, 2002). Natural gaps, formed by the fall of one or more canopy trees, contribute to environmental heterogeneity because they modify the microclimate and alter plant dominance in these sites (Veblen, 1989; Denslow, 1987).

The formation of natural gaps is the most common and best-studied disturbance in forests (Schliemann and Bockheim, 2011). The main differences between gaps and areas with closed canopy are the increase in light incidence and changes in light quality.

In addition, resource availability, such as water and nutrients, can be temporarily increased in gaps (Brandani *et al*., 1988; Denslow, 1980, 1987).

Invasion and dominance by exotic species are well studied in ecology. However, little attention is given to the local expanding native species that negatively affect other native species, which is known as overabundance (Garrot *et al*., 1993), in particular terrestrial herbs, on which there are only few studies in the tropics (Costa, 2004). Good examples of overabundant native species are bamboos (*Guadua* spp.; Lima *et al.,* 2012) and ferns (*Pteridium* spp.; Schneider, 2006; Ribeiro *et al*., 2013), which influence forest structure.

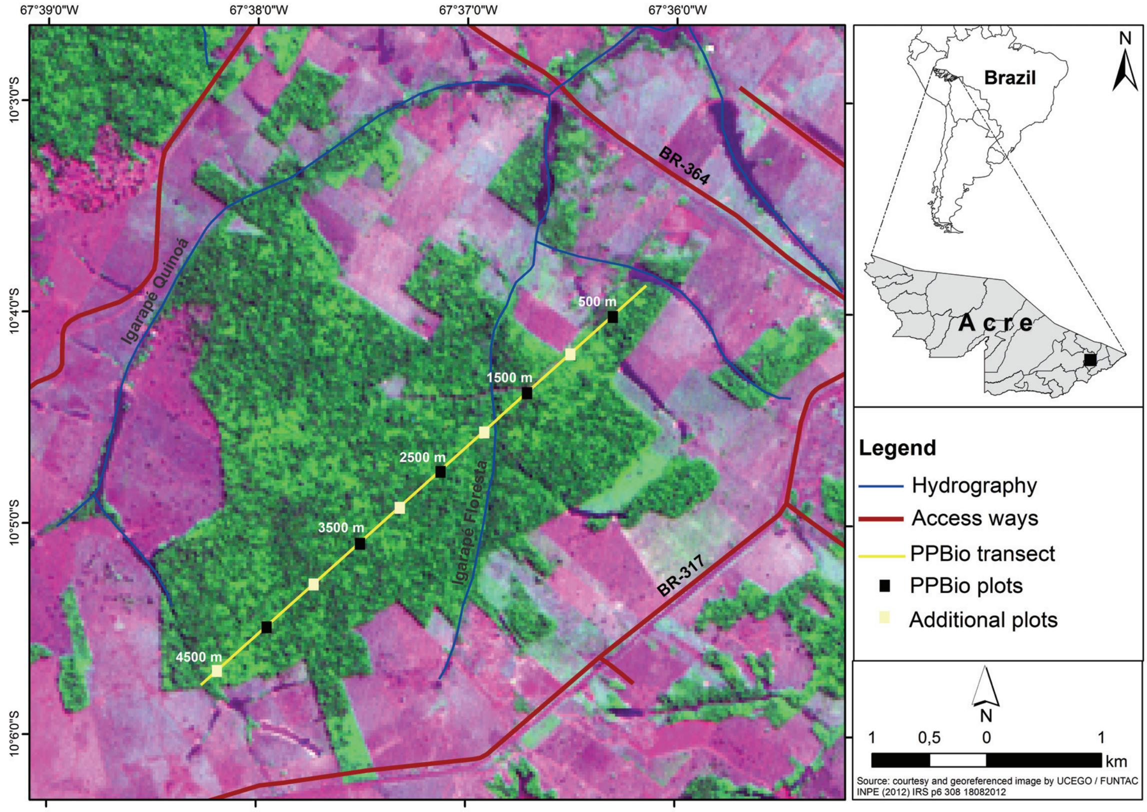
Gentry and Emmons (1987) have identified Maranthaceae as one of the most important families among the understory terrestrial herbs of Neotropical forests. Poulsen and Henrik (1991) and Costa (2004) in their studies have shown the dominance of the species of this family in Amazonian forests of Ecuador and Brazil.

Hence, the objective of the present study was to investigate the regeneration of shrubby-arboreal species in natural gaps in a forest remnant dominated by bamboos (*Guadua weberbaueri* Pilg.) in southwestern Amazon. We aimed at testing whether the abundance of Maranthaceae affects the regeneration of native species in natural gaps.

## Material and methods

### Study area

We carried out the present study at the Catuaba Experimental Farm (CEF), a forest remnant of approximately 1,200 ha, located in Senador Guiomard, state of Acre (Figure 1), northern Brazil



Source: courtesy and georeferenced image by UCEGO / FUNTAC INPE (2012) IRS p6 308 18082012

**Figure 1.** Study area. PPBio plots following the RAPELD protocol, established at the Catuaba Experimental Farm, southwestern Amazonia, Brazil. Each black square indicates the initial position of a 250-m long plot and the yellow squares indicate additional trails marked.

(10°04' S and 67°37' W). The local topography is slightly corrugated, with a predominance of latosols and argisols (Acre, 2006); the horizons A and B are predominantly composed of sand (62 and 47%, respectively); pH approximately 4.0 (Sousa *et al*., 2008). The local altitude is 214 m a.s.l. and the studied forest remnant is located 0.8-7.4 km away from neighbor remnants. It is covered by open rainforest dominated by bamboos (*G. weberbaueri* Pilg.). The local dominant tree species are *Hevea brasiliensis* (WILLD. EX. A. JUSS.) MÜLL.ARG. (Euphobiaceae), *Bertholletia excelsa* HUMB. & BONPL. (Lecythidaceae), *Tetragastris altissima* (AUBL.) SWART (Burseraceae), and *Carapa guianensis* AUBL. (Meliaceae). The canopy height varies from 20 m to 40 m, with emergent trees reaching up to 45 m (Silveira, 2005). The average annual rainfall is 1,958 mm and the average annual temperature is 25 ºC (Duarte, 2006).

For mapping the natural gaps, we walked 10 km of trails, following Runkle (1992), due to standardization for location of natural gaps. We considered all gaps formed by the fall of one or more trees, as well as of part of a tree, in a plot of the Research Program in Biodiversity (PPBio – Programa de Pesquisas em Biodiversidade) established at CEF, following the RAPELD (rapid assessments and long-term ecological research) protocol (Magnusson *et al*., 2005). According to this protocol, a 5 km transect was created, with 10 perpendicular plots (250 m by 20 m width on each side, following the same topographic height), summing 10 plots along the 5 km transect, 500 m apart from each other. In the present study we considered only gaps with a minimum area of 100 m².

### Data sampling

We used the operational definition of gap by Runkle (1981), which includes the area of soil under the canopy opening, extending to the base of adjacent trees. In total, we sampled 20 gaps. We measured the area of each gap with a GPS Garmin 78 (precision of ±4 m), and the percentage of canopy opening with a hemispherical photograph.

In each gap, we installed eight subplots (2 m x 4 m) to represent its heterogeneity (Brandani *et al*., 1988). Inside these subplots, we sampled all shrubby-arboreal plants with height ≥ 1 m and DBH ≤ 10 cm. We marked each individual plant with a numbered plate. We identified the species in the field with the help of a parataxonomist. In addition, we collected samples from each species for identification by comparison with vouchers deposited in the herbarium of the Federal University of Acre (UFAC – Universidade Federal do Acre) and by consulting the specialized literature. Later, the samples were deposited in the collection of the Laboratory of Botany and Plant Ecology of UFAC, Rio Branco, Acre, northern Brazil.

As an operational definition, we considered a Maranthaceae dominated gap when there were one or more Maranthaceae individuals per square meter, since they achieve up to 2m height and long leaves, physically occupying most of the area.

To test for an influence of Maranthaceae abundance on tree regeneration, we counted all individuals in each subplot. Due to the form of growth of these species, we considered each clump as one individual.

### Data analysis

To test for an influence of Maranthaceae abundance on the composition of woody species, we used a non-metric multidimensional scaling analysis (NMDS), using species abundance data and 10,000 permutations. To build the dissimilarity matrix, we used the Bray-Curtis distance.

We used a generalized linear model (GLM) to estimate the influence of Maranthaceae abundance on woody species, by plotting it with the first axis of the NMDS (Maranthaceae as independent variable). Maranthaceae overabundance effect on woody species richness and abundance was also tested with GLM. All analyses were carried out in R environment (R core Team, 2013), using Vegan package (Oksanen *et al.,* 2013).

## Results

The area of the studied gaps varied from 108 to 1,413 m², with an average value of 521 ± 347 m² (average ± Standard Deviation) and a median value of 353 m². The average percentage of canopy opening was 49%; small gaps showed an average canopy opening of 50%, intermediate gaps of 47%, and large gaps of 52%.

We recorded 1,218 shrubby-arboreal individual plants of 145 species, 111 genera, and 45 families (Table 1). The most abundant species were *Piper* sp. (Piperaceae; 16.4%), *Faramea capilipes* MÜLL. ARG. (Rubiaceae; 5.7%), *Tachigali setifera* (DUCKE) ZARUCCHI & HEREND. (Fabaceae; 3.4%), *Brosimum guianense* (AUBL.) HUBER (Moraceae; 3.0%), *Inga* sp. (Fabaceae; 2.5%), *Siparuna guianensis* AUBL. (Siparunaceae; 2.5%), *Guarea* sp. (Meliaceae; 2.3%), *Amphirrhox* sp. (Violaceae; 2.1%), *Eugenia* sp. (Myrtaceae; 2.1%), *Amphiodon effusus* HUBER (Fabaceae; 2.0%), and *Pseudolmedia laevis* (RUIZ & PAV.) J.F.MACBR. (Moraceae; 2.0%).

The NMDS (stress = 0.16) showed a separation between the gaps dominated by Maranthaceae from those not dominated by this family. This result suggests different species composition between gaps with and without dominance of Maranthaceae (Figure 2).

Maranthaceae abundance was marginally correlated with the dissimilarity among gaps, represented by NMDS first axis ($p$ = 0.07, Figure 3). Gaps that are not dominated by Maranthaceae tended to be more dissimilar among each another.

Where there was high dominance of Maranthaceae, there was a significant decrease in the abundance of woody plants, which suggests a negative

**Table 1.** List of species found in natural gaps, in Catuaba Experimental Farm, southwestern Amazonia, Brazil, with their abundance and percentage of gaps in which they were recorded.

| Family | Species | Habit | Gaps occupied (%) | Abundance | Voucher A.S. Maranho* |
|---|---|---|---|---|---|
| Acanthaceae | *Justicia* sp. | Shrub | 5 | 4 | 6209 |
| Achariaceae | *Lindackeria paludosa* (Benth.) Gilg | Shrub | 5 | 1 | 6249 |
| Annonaceae | *Anaxagorea brevipes* Benth. | Tree | 5 | 1 | 6243 |
| | *Duguetia hadrantha* (Diels) R.E.Fr. | Tree | 5 | 1 | 6231 |
| | *Guatteria olivacea* R.E.Fr. | Tree | 20 | 6 | 6223 |
| | *Malmea* sp. | Shrub | 25 | 10 | 6232 |
| | Xylopia sp. | Tree | 5 | 1 | |
| Apocynaceae | *Aspidosperma parvifolium* A.DC. | Tree | 60 | 16 | 6199 |
| | *Aspidosperma rigidum* Rusby | Tree | 5 | 4 | 6200 |
| | *Geissospermum sericeum* Miers | Tree | 5 | 1 | 6307 |
| | *Himatanthus sucuuba* (Spruce ex Müll.Arg.) Woodson | Tree | 10 | 6 | |
| Bignoniaceae | *Handroanthus serratifolius* (A.H.Gentry) S.Grose | Tree | 5 | 1 | |
| Boraginaceae | *Cordia alliodora* (Ruiz & Pav.) Cham. | Tree | 10 | 2 | 6295 |
| | *Cordia nodosa* Lam. | Tree | 25 | 6 | 6296 |
| Burseraceae | *Protium subserratum* (Engl.) Engl. | Tree | 10 | 2 | 6313 |
| | *Tetragastris altissima* (Aubl.) Swart | Tree | 35 | 16 | 6293 |
| Cannabaceae | *Celtis schippii* Trel. ex Standl. | Tree | 45 | 20 | |
| Caricaceae | *Jacaratia spinosa* (Aubl.) A.DC. | Tree | 10 | 3 | 6260 |
| Celastraceae | *Cheiloclinium* sp. Miers | Tree | 5 | 1 | |
| | *Salacia* sp. | | 5 | 1 | 6312 |
| Chrysobalanaceae | *Hirtella racemosa* Lam var. racemosa Lam. | Tree | 55 | 17 | |
| | *Licania caudata* Prance | Tree | 10 | 2 | 6304 |
| Clusiaceae | *Vismia guianensis* (Aubl.) Choisy | Tree | 5 | 1 | 6208 |
| Combretaceae | *Terminalia amazonia* (J.F.Gmel.) Exell | Tree | 5 | 3 | 6252 |
| Ebenaceae | *Diospyros* sp. | Tree | 20 | 4 | 6280 |
| Elaeocarpaceae | *Sloanea guianensis* (Aubl.) Benth. | Tree | 40 | 9 | 6242 |
| Euphorbiaceae | *Acalypha macrostachya* Jacq. | Shrub | 5 | 1 | 6214 |
| | *Conceveiba guianensis* Aubl. | Tree | 5 | 1 | 6206 |
| | *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg. | Tree | 20 | 8 | |
| | *Nealchornea* sp. | Tree | 30 | 14 | 6319 |
| Fabaceae: Caesalpinioideae | *Apuleia leiocarpa* (Vogel) J.F.Macbr. | Tree | 10 | 2 | 6215 |
| | *Barnebydendron riedelii* (Tul.) J.H.Kirkbr. | Tree | 5 | 1 | 6248 |
| | *Dialium guianense* (Aubl.) Sandwith | Tree | 40 | 9 | 6269 |
| | *Hymenaea parvifolia* Huber | Tree | 5 | 1 | 6203 |
| | *Poeppigia procera* C.Presl | Tree | 5 | 1 | 6236 |
| | *Tachigali setifera* (Ducke) Zarucchi & Herend. | Tree | 50 | 41 | 6233 |
| Fabaceae: Faboideae | *Amphiodon effusus* Huber | Tree | 50 | 24 | 6281 |

**Table 1.** Continuation.

| Family | Species | Habit | Gaps occupied (%) | Abundance | Voucher A.S. Maranho* |
|---|---|---|---|---|---|
| | *Bowdichia* sp. | Tree | 10 | 2 | 6198 |
| | *Erythrina* sp. | Tree | 15 | 4 | |
| | *Myroxylon balsamum* (L.) Harms | Tree | 5 | 1 | 6286 |
| | *Ormosia* sp. | Tree | 15 | 3 | 6278 |
| | *Pterocarpus amazonum* (Benth.) Amshoff | Tree | 15 | 4 | 6210 |
| | *Swartzia oraria* R.S.Cowan | Tree | 25 | 5 | 6265 |
| | *Swartzia* sp. | Tree | 5 | 2 | 6266 |
| | *Vatairea fusca* (Ducke) Ducke | Tree | 5 | 1 | 6211 |
| Fabaceae: Mimosoideae | *Abarema laeta* (Benth.) Barneby & J.W.Grimes | Tree | 5 | 1 | 6283 |
| | *Anadenanthera* sp. | | 5 | 1 | |
| | *Enterolobium maximum* Ducke | Tree | 5 | 1 | 6193 |
| | *Inga cylindrica* (Vell.) Mart. | Tree | 5 | 1 | 6235 |
| | *Inga* sp. 1 | Tree | 5 | 1 | |
| | *Inga* sp. 2 | Tree | 40 | 11 | 6320 |
| | *Inga* sp. 3 | Tree | 15 | 4 | 6196 |
| | *Inga* sp. 4 | Tree | 55 | 31 | |
| | *Stryphnodendron guianense* (Aubl.) Benth. | Tree | 5 | 1 | 6258 |
| | Mimosoideae 1 | | 5 | 1 | |
| | Mimosoideae 2 | | 5 | 1 | |
| | Mimosoideae. 3 | Tree | 30 | 9 | |
| Lauraceae | *Endlicheria* sp. | Tree | 5 | 1 | 6221 |
| | *Mezilaurus sprucei* (Meisn.) Taub. ex Mez | Tree | 20 | 4 | 6212 |
| | *Ocotea oblonga* (Meisn.) Mez | Tree | 5 | 1 | 6297 |
| | *Ocotea* sp. 2 | Tree | 30 | 7 | 6254 |
| | *Ocotea* sp. | Tree | 15 | 3 | 6317 |
| Lecythidaceae | *Couratari guianensis* Aubl. | Tree | 40 | 15 | 6234 |
| | *Eschweilera coriacea* (DC.) S.A.Mori | Tree | 15 | 3 | |
| | *Eschweilera truncata* A.C.Sm. | Tree | 20 | 4 | 6225 |
| | *Gustavia augusta* L. | Tree | 40 | 17 | 6253 |
| Malvaceae | *Herrania nitida* (Poepp.) R.E.Schult. | Tree | 10 | 2 | 6279 |
| | *Pseudobombax munguba* (Mart. & Zucc.) Dugand | Tree | 10 | 2 | 6207 |
| | *Quararibea guianensis* Aubl. | Tree | 70 | 21 | 6267 |
| | *Sterculia* sp. | Tree | 5 | 1 | 6244 |
| | *Theobroma obovatum* Klotzsch ex Bernoulli | Tree | 45 | 19 | 6230 |
| | *Huberodendron swietenioides* (Gleason) Ducke | Tree | 10 | 2 | 6213 |
| Melastomataceae | *Miconia affinis* DC. | Shrub | 10 | 3 | 6259 |
| | *Miconia* sp. | | 5 | 4 | |
| | *Mouriri myrtifolia* Spruce ex Triana | Tree | 20 | 7 | 6216 |

**Table 1.** Continuation.

| Family | Species | Habit | Gaps occupied (%) | Abundance | Voucher A.S. Maranho* |
|---|---|---|---|---|---|
| Meliaceae | *Guarea* sp. | Tree | 65 | 28 | 6322 |
| | *Trichilia pleeana* (A.Juss.) C.DC. | Tree | 15 | 3 | 6247 |
| Moraceae | *Brosimum guianense* (Aubl.) Huber | Tree | 70 | 37 | 6264 |
| | *Brosimum lactescens* (S.Moore) C.C.Berg | Tree | 5 | 1 | 6224 |
| | *Castilla ulei* Warb. | Tree | 5 | 1 | |
| | *Clarisia ilicifolia* (Spreng.) Lanj. & Rossberg | Tree | 45 | 19 | 6276 |
| | *Clarisia racemosa* Ruiz & Pav. | Tree | 15 | 4 | 6239 |
| | *Naucleopsis glabra* Spruce ex Pittier | Tree | 45 | 12 | 6270 |
| | *Perebea mollis* (Poepp. & Endl.) Huber | Tree | 45 | 14 | 6268 |
| | *Pseudolmedia laevis* (Ruiz & Pav.) J.F.Macbr. | Tree | 55 | 24 | 6323 |
| | *Pseudolmedia macrophylla* Trécul | Tree | 10 | 2 | 6299 |
| | *Sorocea muriculata* Miq. | Tree | 5 | 1 | 6192 |
| | *Sorocea* sp. | Tree | 60 | 22 | 6238 |
| Myristicaceae | *Compsoneura ulei* Warb. | Tree | 15 | 3 | 6277 |
| | *Iryanthera juruensis* Warb. | Tree | 10 | 2 | 6255 |
| | *Virola multinervia* Ducke | Tree | 25 | 6 | 6227 |
| | *Virola* sp. 2 | Tree | 5 | 1 | 6257 |
| | *Virola* sp. | Tree | 5 | 1 | 6191 |
| Myrtaceae | *Eugenia* sp. 1 | Tree | 5 | 1 | |
| | *Eugenia acrensis* McVaugh | Tree | 5 | 1 | 6300 |
| | *Eugenia* sp. 2 | Tree | 65 | 26 | 6282 |
| Nyctaginaceae | *Neea floribunda* Poepp. & Endl. | Tree | 55 | 23 | |
| | *Neea* sp. 1 | Tree | 5 | 1 | |
| | *Neea* sp. 2 | Tree | 15 | 3 | 6217 |
| Olacaceae | *Aptandra tubicina* (Poepp.) Benth. ex Miers | Tree | 10 | 2 | 6226 |
| | *Chaunochiton* sp. | Tree | 10 | 2 | 6195 |
| | *Heisteria duckei* Sleumer | Tree | 10 | 2 | 6263 |
| | *Minquartia guianensis* Aubl. | Tree | 10 | 2 | 6205 |
| Piperaceae | *Piper arboreum* Aubl. | Shrub | 15 | 5 | |
| | *Piper hispidinervum* C.DC. | Shrub | 30 | 7 | 6289 |
| | *Piper* sp. 1 | Shrub | 90 | 200 | 6273 |
| | *Piper* sp. 2 | Shrub | 30 | 13 | 6315 |
| | *Piper* sp. 3 | Shrub | 15 | 4 | 6314 |
| Polygonaceae | Triplaris sp. | Tree | 20 | 7 | |
| Primulaceae | *Cybianthus guyanensis* subsp. *pseudoicacoreus* (Miq.) Pipoly | Tree | 5 | 1 | 6251 |
| Putranjivaceae | *Drypetes amazonica* Steyerm. | Tree | 25 | 5 | 6308 |
| Rubiaceae | *Alibertia claviflora* K.Schum. | Tree | 5 | 1 | 6294 |
| | *Alseis* sp. | | 5 | 1 | 6309 |

**Table 1.** Continuation.

| Family | Species | Habit | Gaps occupied (%) | Abundance | Voucher A.S. Maranho* |
|---|---|---|---|---|---|
| | *Amaioua guianensis* Aubl. | Tree | 5 | 1 | 6311 |
| | *Capirona decorticans* Spruce | Tree | 5 | 4 | 6262 |
| | *Faramea capillipes* Müll. Arg. | Tree | 80 | 70 | 6229 |
| | Rubiaceae | | 10 | 3 | |
| | *Palicourea* sp. | Tree | 20 | 8 | 6285 |
| | *Psychotria hoffmannseggiana* (Willd. ex Schult.) Müll. Arg. | Shrub | 25 | 9 | 6197 |
| | *Psychotria lupulina* Benth. | Shrub | 5 | 1 | 6190 |
| | *Psychotria* sp. 1 | Shrub | 30 | 10 | |
| | *Psychotria* sp. 2 | Shrub | 5 | 2 | 6201 |
| Rutaceae | *Metrodorea flavida* K.Krause | Tree | 10 | 2 | 6261 |
| Salicaceae | *Banara nitida* Spruce ex Benth. | Tree | 10 | 2 | 6194 |
| | *Casearia gossypiosperma* Briq. | Tree | 20 | 4 | 6202 |
| Sapindaceae | *Allophylus pilosus* (J.F.Macbr.) A.H.Gentry | Tree | 30 | 22 | 6237 |
| | *Talisia cerasina* (Benth.) Radlk. | Shrub | 10 | 3 | 6290 |
| Sapotaceae | *Pouteria caimito* (Ruiz & Pav.) Radlk. | Tree | 25 | 11 | 6272 |
| | *Pouteria campanulata* Baehni | Tree | 5 | 1 | 6204 |
| | *Pouteria hispida* Eyma | Tree | 15 | 4 | 6291 |
| | *Pouteria* sp. 1 | Tree | 10 | 2 | 6298 |
| | *Pouteria* sp. 2 | Tree | 5 | 1 | |
| | *Pradosia atroviolacea* Ducke | Tree | 25 | 8 | 6245 |
| Siparunaceae | *Siparuna guianensis* Aubl. | Tree | 65 | 31 | 6274 |
| Solanaceae | *Brunfelsia grandiflora* D.Don | Shrub | 25 | 5 | 6241 |
| Thymelaeaceae | *Schoenobiblus peruviana* Standl. | Tree | 10 | 2 | 6301 |
| Ulmaceae | *Ampelocera* sp. | Tree | 15 | 3 | |
| Urticaceae | *Pourouma cecropiifolia* Mart. | Tree | 5 | 1 | 6287 |
| | *Pourouma guianensis* Aubl. | Tree | 15 | 7 | 6292 |
| | *Pourouma minor* Benoist | Tree | 50 | 11 | 6275 |
| | *Urera* sp. | | 10 | 2 | |
| Violaceae | *Amphirrhox* sp. | Tree | 75 | 26 | 6271 |
| | *Leonia glycycarpa* Ruiz & Pav. | Tree | 30 | 10 | 6218 |
| | *Rinoreocarpus ulei* (Melch.) Ducke | Tree | 40 | 15 | 6222 |
| Vochysiaceae | *Qualea grandiflora* Mart. | Tree | 15 | 6 | 6256 |
| Total | | | | 1,218 | |

Note: (*) initial code tipping specimens.

linear relationship (GLM, $p < 0.001$; $r^2=0.58$; Figure 4A). The local richness also decreased in areas dominated by Maranthaceae (GLM, $p = 0.001$, $r^2=0.48$; Figure 4B). Therefore, there was an increase in dissimilarity between areas dominated and areas not dominated by Maranthaceae, as the abundance of individuals of this family increased. The decrease in woody species abundance and richness in areas dominated by Maranthaceae can result from competition for space, explained by the extensive soil cover by Maranthaceae individuals (Figure 5).

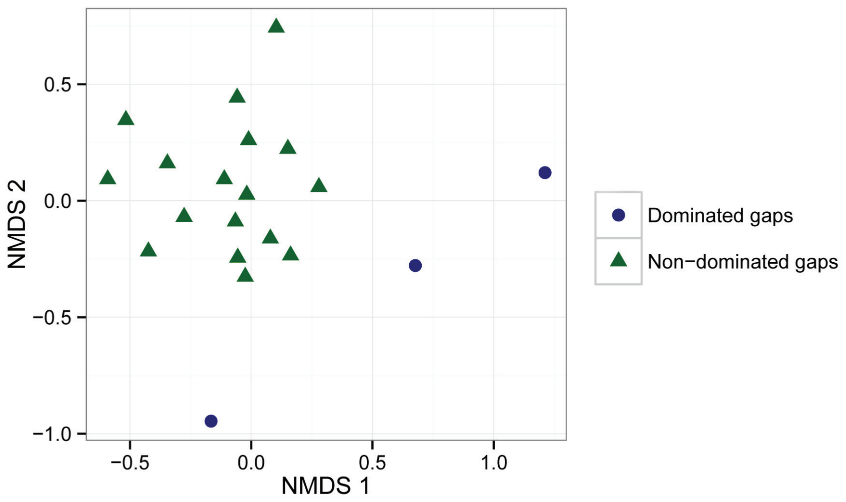


**Figure 2.** NMDS based on species composition of natural gaps, in Catuaba Experimental Farm, southwestern Amazonia, Brazil, grouped by dominance of Maranthaceae.

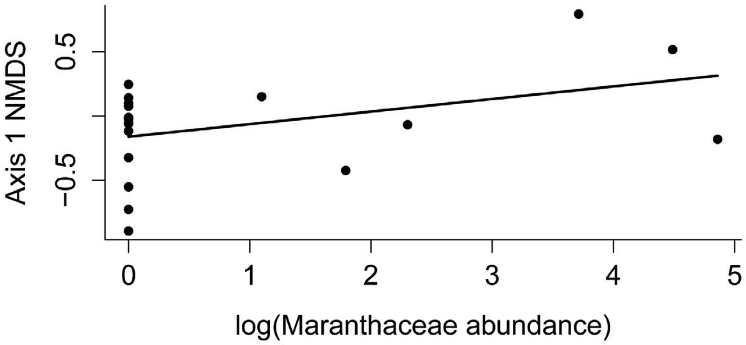


**Figure 3.** GLM between the axis 1 of the NMDS and Maranthaceae abundance ($p$ = 0.07) in gaps with or without dominance by Maranthaceae in Catuaba Experimental Farm, southwestern Amazonia, Brazil.

## Discussion

In the present study, the overabundance of Maranthaceae decreased the abundance and richness of woody plants. Therefore, the gaps dominated by this family differed in species composition from the gaps not dominated by it. Similar results were presented by Lima and Moura (2006), who briefly reported the occurrence of two genera of Maranthaceae (*Calathea* and *Ctenanthe*) in forest gaps in the Atlantic Forest. These authors suggest that the wide leaves and the habit of forming dense clumps could produce a thick leaf litter, which could hinder the germination of other plants. Although not measured in the present study, we observed that where Maranthaceae are dense, their leaf litter also form a thick layer on soil, which could have the same effect as presented experimentally by Santos and Válio (2002) who showed the effect of litter on seedling recruitment and revealed the importance of film thickness in obstructing seedling emergence.

According to Costa (2004), among the terrestrial herbs found in the *terra firme* forest in Central Amazonia, the family Maranthaceae was one of the richest in species and contributed strongly to soil cover when compared with the other herbs studied. In light of this, in gaps where Maranthaceae occurred and were dominant, such dense patches could form by the inhi-

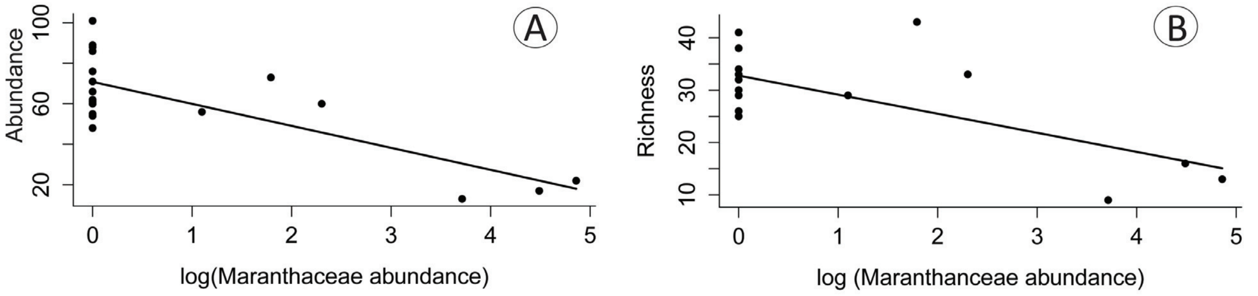


**Figure 4.** Species abundance (A) and richness (B) of woody plants as a function of Maranthaceae abundance in Maranthaceae dominated and non-dominated gaps in Catuaba Experimental Farm, southwestern Amazonia, Brazil.

**Figure 5.** Natural gaps with dominance by Maranthaceae, in the Catuaba Experimental Farm, southwestern Amazonia, Brazil. (A) A gap opening by a single tree fall; (B) a typical Maranthaceae; (C) a Maranthaceae dominated gap.

bition model of succession elucidated by Connell and Slatyer (1977). On the other hand, one must keep in mind that such colonization and dominance may also have occurred by mere stochastic events, such as the existence of seed dispersal in the time of gap opening and not because these species are more adapted than others to such gap environments.

We observed that Maranthaceae occurs in patches and seems to be favored by gap opening and the presence of watercourses. According to Costa and Magnusson (2002), gap opening and increase in light incidence can lead to an increase in the abundance of some herbaceous species, an effect observed in some Maranthaceae species. Costa *et al*. (2005) observed that the structure of the herbaceous community, in particular of Maranthaceae, is also strongly affected by the type of soil and the presence of clay.

Such results could be caused by many factors, but the most probable cause of decrease in woody species abundance and richness is the competition for space. Gaps dominated by Maranthaceae had less physical space for other individuals' establishment. With such argument in mind, it would be desirable to understand and determine which the main factors controlling distribution and occurrence of Maranthaceae in these forests are.

## Conclusions

Maranthaceae overabundance decreased woody species abundance and richness significantly, which was corroborated by the dissimilarity among dominated and non-dominated gaps.

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