



# Woody flora of natural forest gaps in a bamboo-dominated forest remnant in southwestern Amazonia

Álison Sobrinho Maranhão<sup>1\*</sup>, Cleber Ibraim Salimon<sup>1,2</sup> and Daniel da Silva Costa<sup>3</sup>

1 Universidade Federal do Acre, Programa de Pós-Graduação em Ecologia e Manejo de Recursos Naturais, BR-364, Distrito Industrial, CEP 69920-900, Rio Branco, AC, Brazil

2 Universidade Estadual da Paraíba, Rua Horácio Trajano de Oliveira, CEP 58020-540, João Pessoa, PB, Brazil

3 Universidade Federal do Acre, Centro de Ciências Biológicas e da Natureza, BR-364, Distrito Industrial, CEP 69920-900, Rio Branco, AC, Brazil

\* Corresponding author. E-mail: [alissonsobrinho@hotmail.com](mailto:alissonsobrinho@hotmail.com)

**Abstract:** Forest gaps, created by the falling of one or more trees, have been seen as a key factor for the maintenance of local plant diversity in tropical forests. In this study, our goal was to determine the floristic composition of woody plants colonizing natural gaps and in the understory of an open, bamboo-dominated (*Guadua weberbaueri* Pilg.) forest in southwestern Amazonia, Acre, Brazil. We sampled and identified woody plants ( $\geq 1$  m tall and  $DBH \leq 10$  cm) in 20 forest gaps and nine adjacent understories. In total, 1656 plants were identified in 159 species, 116 genera and 45 families. A list of species was created, containing habitat, habit, functional group, threat status (Brazilian Flora Red List) and abundance data for each species.

**Key words:** alpha diversity; forest regeneration; functional group; *Guadua*; treefall gaps

## INTRODUCTION

Tropical forests have the greatest plant diversity in our planet (Dirzo and Raven 2003). Recent estimates point that the Amazon is the home for approximately 16,000 tree species ( $DBH \geq 10$  cm), from which 227 are superdominant, because they are much more abundant than the other species (Ter Steege et al. 2013). Despite this information and knowledge, few studies address species richness during regeneration in Amazonian forests.

Canopy gaps formed by one or more falling trees (Runkle 1992) are the most common and studied type of forest disturbance (Schliemann and Bockheim 2011) and are also thought to be one of the major drivers of species diversity at the local scale (Connell 1978). Nevertheless, recent studies have shown some divergence in the application of this hypothesis, suggesting that canopy gaps play a relative neutral role in the maintenance of diversity, mediating the limitation effect upon

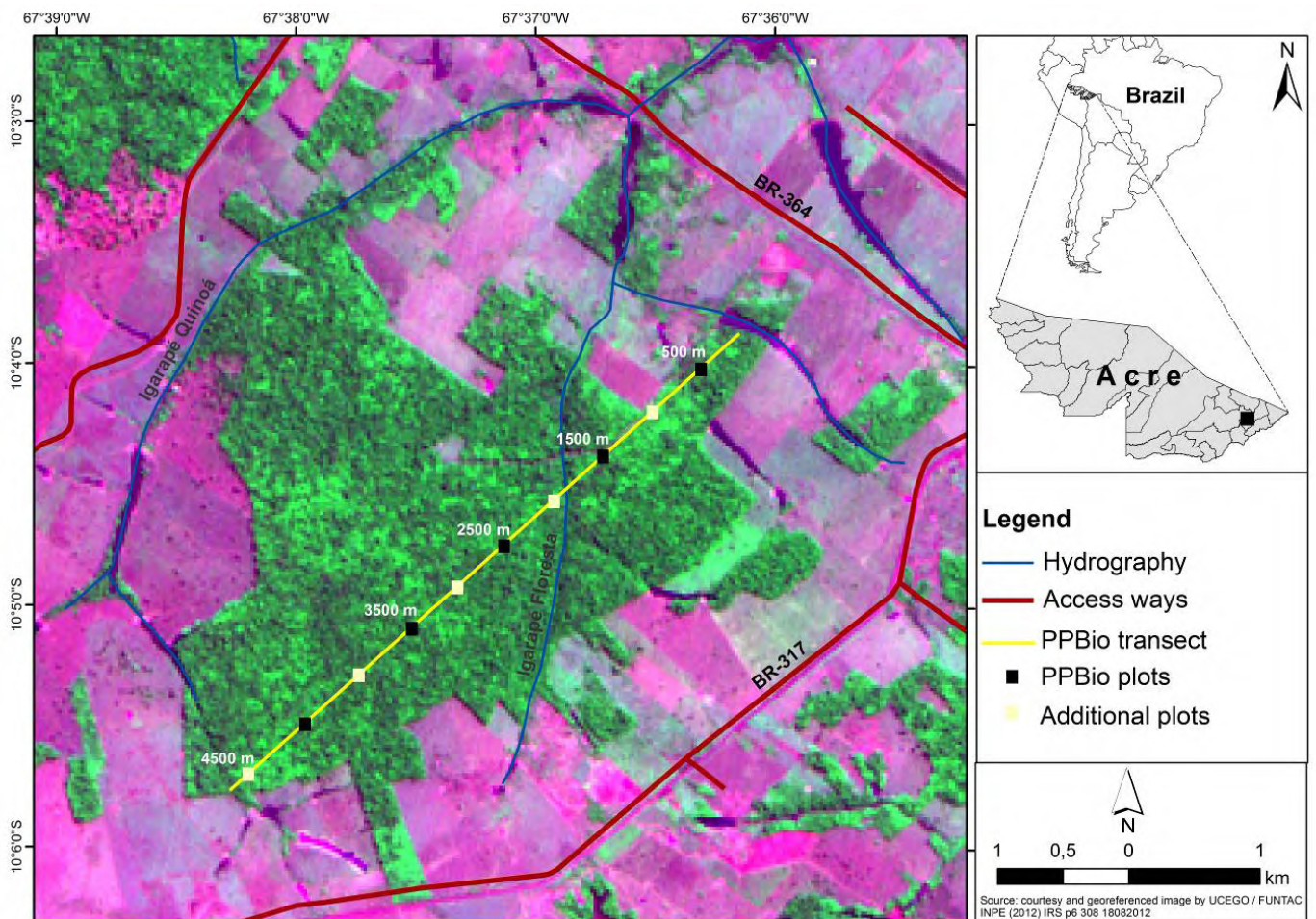
recruitment (Hubbell et al. 1999; Sheil and Burslem 2003; Obiri and Lawes 2004; Fox 2013). Other studies also associate gap area and heterogeneity with tree species composition (Brokaw 1985; Denslow 1987; Brokaw and Scheiner 1989).

Bamboo (*Guadua* spp.) dominated forests cover more than half of southwestern Amazonia (Carvalho et al. 2013). These are considered uncommon and differ structural and floristically from closed canopy forests in central and eastern Amazonia (Torezan and Silveira 2000; Griscom and Ashton 2003, 2006; Griscom et al. 2007). Still, although these studies address regeneration patterns under the influence of bamboo, there is still little information about composition and diversity in natural gaps in these bamboo-dominated forests.

Our goal in this paper was to identify the floristic composition and to analyze the structure of regenerating woody plants in natural forest gaps and adjacent understory in a bamboo dominated forest remnant in southwestern Amazonia, Acre, Brazil. Our findings will increase the knowledge of the composition of species after gap opening in such forests, where there is scant literature about it.

## MATERIALS AND METHODS

This study was carried out at the Catuaba Experimental Farm (FEC; Figure 1), a forest fragment with ca. 1,200 ha located in the state of Acre, Brazil ( $10^{\circ}04' S$ ,  $067^{\circ}37' W$ ). It has a gently rolling topography with predominance of oxisols and ultisols (Acre 2006); horizons A and B are predominantly sandy (62 and 47%, respectively); pH approximately 4.0 (Sousa et al. 2008). Its altitude is 214 m above sea level and is 0.8 to 7.4 km away from neighboring remnants. The area is covered by bamboo (*Guadua weberbaueri* Pilg.) dominated open rainforest. The dominant trees are *Hevea brasiliensis* (Willd. ex A. Juss.) Müll.Arg. (Euphorbiaceae), *Bertholletia excelsa*



**Figure 1.** PPBio's plots following RAPELD protocol, in the Fazenda Experimental Catuaba. Each black dot identifies a 250m trail/plot (following RAPELD's protocol for PPBio) and addition trails are yellow dot between the black dots.

Humb. & Bonpl. (Lecythidaceae), *Tetragastris altissima* (Aubl.) Swart (Burseraceae) and *Carapa guianensis* Aubl. (Meliaceae). Canopy height varies from 20 to 40 m, with emergent trees up to 45 m (Silveira 2005). Mean annual rainfall is 1,958 mm and average annual temperature is 25°C (Duarte 2006). We surveyed forest gaps in this fragment and walked through 10 km of trails, following Runkle's method (1992). All gaps formed by the fall of one or more trees in a PPBio module (Programa de Pesquisas em Biodiversidade), established at FEC, following RAPELD protocols (Magnusson et al. 2005). Only gaps  $\geq 100 \text{ m}^2$  were included in our study.

We applied Runkle's operational definition of a gap, which includes the soil area under the canopy opening, extending to the trunk of the adjacent trees. We surveyed 20 gaps. In each gap, we established eight subplots ( $2 \times 4 \text{ m}$ ) following Brandani et al. (1988). For the understory, we randomly selected nine gaps (from the initial 20) and about 20 m away from each gap edge, we plotted a  $2 \times 32 \text{ m}$  plot, divided in eight subplots of  $2 \times 4 \text{ m}$ .

In each subplot (both gaps and understory) all woody plants  $\geq 1 \text{ m}$  tall and with  $\text{DBH} \leq 10 \text{ cm}$  were sampled. Each plant was marked with a numbered tag.

Plant identification was first made in the field with the aid of an experienced parataxonomist. Also, we sampled from all morphotypes identified in the field as a species for identification in the herbarium, based on the Angiosperm Phylogeny Group (APG III 2009). In order to check for proper species names spelling, we used the Brazilian Flora List (Flora do Brasil 2020, under construction, 2016). All fertile samples had their vouchers incorporated in the collection of the Botany and Plant Ecology Laboratory (LABEV) of the Federal University of Acre, Rio Branco, Acre, Brazil. Sterile specimens were not incorporated at the herbarium.

All species were classified in four functional groups, mainly due to its light necessity, which are: pioneers, early and late secondary species and "unclassified" (Budowski 1965; Denslow 1980). A description of each of these categories can be accessed in Gandolfi (2000). The classification of each species was made by literature consultation (Amaral et al. 2009; Denslow 1980; Gandolfi 2000; Gargiullo et al. 2008; Lorenzi 2008; 2009; Oliveira 2011; Santos 2013; Silva 2011) and also by the use of a functional group list, developed by the Botany and Plant Ecology Laboratory of the Federal

University of Acre (LABEV), based on forest inventories and species identification and classification under the project “Casadinho” (unpublished data, CNPq grant number 620236/2006-0).

Species were also classified into conservation or threat status in agreement with the Brazilian Flora Red List (Martinelli and Moraes 2013).

To analyze the structure of regeneration in both environments abundance of species distribution curves were constructed (species abundance distribution: SAD), through the rank of the most abundant species for rarer (McGill et al. 2007; Matthews and Whittaker 2014). The length of the curves allows analyzing the species richness using the x-axis; and the slope allows an analysis of evenness among species, by reading the axis of ordinates. In this sense more inclined curves and smaller have fewer species and most dominant (Magurran 2005). To test whether there are differences between the SAD curves we used the Kolmogorov-Smirnov test.

Analyzes were performed with R software (R Core Team, 2013), using Vegan 2.2 package (Oksanen et al. 2013).

## RESULTS

The average gap area was  $521 \pm 347 \text{ m}^2$ , ranging from 108 to  $1,413 \text{ m}^2$ , median  $353 \text{ m}^2$ . Total gap area was  $10,429 \text{ m}^2$ . The average canopy openness was 49%, while for small, medium and large gaps it was 50%, 47% and 52% respectively. Forest understory showed an average of 14% of canopy openness and was significantly ( $F=11.05$ ;  $p<0.001$ ) different from gaps, which did not differ among each other.

We sampled 1,656 shrubs and trees, 159 species, 116 genera and 45 families in both gaps and understory (Table 1). Sixty-two species were found only in gaps and 14 only in the understory. Eighty-six species co-occurred in gaps and understory. Eighty-three percent of the species are trees, 11% are shrubs and 6% were not classified in any habit due to lack of species identification. Many species were rare, with 41 sampled only once and 23 just twice.

The most speciose families were Fabaceae (27 species, from all three subfamilies) comprising 17% of species richness; Rubiaceae (13); Moraceae (12); Lauraceae, Malvaceae and Sapotaceae (7). Four families were represented by two species and 19 families had only one species each. Piperaceae showed the highest number of individuals, comprising 15% of total abundance. Together, Piperaceae, Fabaceae, Moraceae and Rubiaceae hold 49% of all plants sampled.

For the forest as a whole (gaps and understory), the species with highest relative abundance were *Piper* sp. 1 (13.0%), *Faramea capillipes* Müll. Arg. (5.1%), *Tachigali setifera* (Ducke) Zarucchi & Herend. (3.5%), *Brosimum guianense* (Aubl.) Huber (3.2%), *Eugenia* sp. 2 (3.1%),

*Guarea* sp. (2.5%), *Pseudolmedia laevis* (Ruiz & Pav.) J.F.Macbr. (2.4%), *Inga* sp. 4 (2.4%), *Amphirrhox* sp. (2.3%), *Siparuna guianensis* Aubl. (2.2%), *Neea floribunda* Poepp. & Endl. (2.2%) and *Celtis schippii* Trel. ex Standl. (2.1%). From these most abundant species, three were also found to be the most frequent genera regenerating in the same forest fragment: *Neea*, *Guarea* and *Celtis* (Silva 2011).

Some of the species showed gap dependence for regeneration, showing a much greater abundance in gaps. *Piper* sp. 1 had 93% of its individuals in gaps, *Faramea capillipes* 83%, *Tachigali setifera* and *Brosimum guianense* with 69% of their individuals in gaps as well. On the other hand, only two species were found mainly or solely in the understory, *Compsoeura ulei* Warb. (63%) and *Randia armata* (Sw.) DC. (100%). Nevertheless, most species did not present any pattern or preference for either gaps or understory (Table 1).

Table 1 shows also the threat status of each species sampled at FEC. Only three species are classified as “vulnerable VU”, which according to the Red List (Martinelli and Moraes 2013), face a high risk of extinction in the wild. Six other species were classified as “least concern LC”, which means there is lack of information available now, but could be included in VU with further studies (Martinelli and Moraes 2013).

Figure 2 shows the species abundance distribution (SAD) within the gaps and the understory. The Kolmogorov-Smirnov test showed that there is a structural difference between the two environments ( $p<0.001$ ).

## DISCUSSION

The results shown here for Fabaceae are characteristic of Amazonian forests, where the family presents the highest diversity and abundance (Steege et al. 2013). For the genus *Piper*, such high relative abundance in gaps was expected since species from this genus are known to be light dependent, have higher growth rates and more abundant in natural gaps (Denslow et al. 1990; Daws et al. 2002; Bernades and Costa 2011).

Differences in abundance and dominance of species rank (Figure 2) will indicate structural differences, which are modified on the environment and their colonization by different species, caused by disturbance when the formation of natural gaps (Connel 1978; Connel and Green 2000; Denslow 1987, 1995). The curve of species distribution that occurred in clearings is steeper than the abundance curve of the understory. This shows that the dominance is higher in gaps, caused by the abundance of the species *Piper* sp. 1 and *Faramea capillipes*. In understory only *Eugenia* sp. 2 has mild dominance. In this sense, the distribution of abundances of species of understory is more evenness compared with clearings.

The three vulnerable species (Table 1; *Apuleia leiocarpa*

Table 1. Tree and Shrub flora and abundance, occurring in natural gaps and understory in a forest fragment in the Fazenda Experimental Catuaba, Senador Guiomard, Acre Brazil.

Family	Species	Common names	Abundance	Habitat <sup>1</sup>	Habitat	Functional groups <sup>2</sup>	Threat status <sup>3</sup>	Voucher
Acanthaceae	<i>Justicia</i> sp.		4	G	Shrub	UN		A.S. Maranho 6209
Achariaceae	<i>Lindackeria paludosa</i> (Benth.) Gilg		3	G & U	Shrub	UN		A.S. Maranho 6249
Annonaceae	<i>Anaxagorea brevipes</i> Benth.		1	G	Tree	ES		A.S. Maranho 6243
	<i>Duguetia hadrantha</i> (Diels) R.E.Fr.	Ata	2	G & U	Tree	UN		A.S. Maranho 6231
	<i>Guatteria olivacea</i> R.E.Fr.	Envira fofa	10	G & U	Tree	UN		A.S. Maranho 6223
	<i>Malmea</i> sp.	Envreira	16	G & U	Shrub	UN		A.S. Maranho 6232
	<i>Xylopia</i> sp.	Envira fofa	2	G & U	Tree	UN		
Apocynaceae	<i>Aspidosperma parvifolium</i> A.DC.	Amaralão	23	G & U	Tree	ES		A.S. Maranho 6199
	<i>Aspidosperma rigidum</i> Rusby	Carapanatuba amarela	6	G & U	Tree	ES		A.S. Maranho 6200
	<i>Geispermium sericeum</i> Miels	Quina quina amarela	3	G & U	Tree	ES		A.S. Maranho 6307
	<i>Himatanthus sucuba</i> (Spruce ex Müll.Arg.) Woodson	Sucuuba	7	G & U	Tree	ES		H. Medeiros 1743
Bignoniaceae	<i>Handroanthus serratifolius</i> (A.H.Gentry) S.Grose	Pau d'arco amarelo	2	G & U	Tree	ES		A.S. Maranho 6295
Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Cham.	Freijó preto	2	G	Tree	ES		A.S. Maranho 6296
	<i>Cordia nodosa</i> Lam.	Freijó branco	8	G & U	Tree	P		A.S. Maranho 6313
Burseraceae	<i>Protium subserratum</i> (Engl.) Engl.	Breuzinho de capoeira	2	G	Tree	ES		H. Medeiros 1687
	<i>Protium unifoliolatum</i> Engl.	Breu	1	U	Tree	ES		A.S. Maranho 6293
Cannabaceae	<i>Tetragastris altissima</i> (Aubl.) Swart	Breu vermelho	28	G & U	Tree	LS		R.S. Saraiva 3925
Caricaceae	<i>Celtis schippii</i> Trel. ex Standl.	Farinha seca	34	G & U	Tree	UN		A.S. Maranho 6260
Celastraceae	<i>Jacaratia spinosa</i> (Aubl.) A.DC.	Jaracatiá	3	G	Tree	P	LC	
	<i>Cheiloclinium</i> sp.		1	G	Tree	UN		
	<i>Salacia</i> sp.		1	G	Tree	UN		A.S. Maranho 6312
Chrysobalanaceae	<i>Hirtella racemosa</i> var. <i>racemosa</i> Lam.	Macucu mirim	25	G & U	Tree	LS	LC	D.C. Daly 5544
	<i>Licania caudata</i> Prance	Macucu	5	G & U	Tree	LS		A.S. Maranho 6304
Clusiaceae	<i>Vismia guianensis</i> (Aubl.) Choisy	Lacre	1	G	Tree	P		A.S. Maranho 6208
Combretaceae	<i>Terminalia amazonia</i> (J.F.Gmel.) Exell	Mirindiba amarela	3	G	Tree	LS		A.S. Maranho 6252
Ebenaceae	<i>Diospyros</i> sp.	Sete camadas	5	G & U	Tree	UN		A.S. Maranho 6280
Elaeocarpaceae	<i>Sloanea guianensis</i> (Aubl.) Benth.	Urucuruana	13	G & U	Tree	ES		A.S. Maranho 6242
Euphorbiaceae	<i>Acalypha macrostachya</i> Jacq.		1	G	Shrub	P		A.S. Maranho 6214
	<i>Aparisthium cordatum</i> (A.Juss.) Baill.	Marmelo	1	U	Tree	P		A.S. Maranho 6302
	<i>Conceveiba guianensis</i> Aubl.	Breu branco	1	G	Tree	LS		A.S. Maranho 6206
	<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	Seringueira	10	G & U	Tree	LS		M. Silveira 3120
	<i>Nealchornea</i> sp.		14	G	Tree	UN		A.S. Maranho 6319
Fabaceae: Caesalpinioideae	<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	Cumaru cetim	2	G	Tree	ES	VU	A.S. Maranho 6215
	<i>Barbeydendron riedelii</i> (Tul.) J.H.Kirkbr.	Guaribeiro	1	G	Tree	LS		A.S. Maranho 6248
	<i>Dialium guianense</i> (Aubl.) Sandwith	Tamarindo	15	G & U	Tree	LS		A.S. Maranho 6269
	<i>Hymenaea parvifolia</i> Huber	Jutaí	1	G	Tree	LS	VU	A.S. Maranho 6203
	<i>Poeppigia procera</i> C.Presl	Pintadinho	1	G	Tree	ES		A.S. Maranho 6236
	<i>Tachigali</i> sp.	Tachi peludo	1	U	Tree	UN		A.S. Maranho 6305
	<i>Tachigali setifera</i> (Ducke) Zarucchi & Herend.	Tachi vermelho	59	G & U	Tree	ES		A.S. Maranho 6233
Fabaceae: Faboideae	<i>Amphiodon effusus</i> Huber	Sucupira mirim	30	G & U	Tree	LS		A.S. Maranho 6281

Continued

Table 1. Continued.

Family	Species	Common names	Abundance	Habitat <sup>1</sup>	Habitat	Functional groups <sup>2</sup>	Threat status <sup>3</sup>	Voucher
	<i>Bowdichia</i> sp.	Sucupira preta	2	G	Tree	UN		A.S. Maranho 6198
	<i>Erythrina</i> sp.	Mulungu vermelho	4	G	Tree	UN		
	<i>Myroxylon balsamum</i> (L.) Harms	Bálsamo	1	G	Tree	ES		A.S. Maranho 6286
	<i>Ormosia</i> sp.	Mulungu vermelho	5	G & U	Tree	UN		A.S. Maranho 6278
	<i>Pterocarpus amazonum</i> (Benth.) Amshoff	Pau sangue de casca fina	4	G	Tree	ES		A.S. Maranho 6210
	<i>Swartzia oraria</i> R.S.Cowan	Pitaica	8	G & U	Tree	LS		A.S. Maranho 6265
	<i>Swartzia</i> sp.		2	G	Tree	UN		A.S. Maranho 6266
	<i>Vatairea fusca</i> (Ducke) Ducke	Amargoso	1	G	Tree	UN		A.S. Maranho 6211
Fabaceae: Mimosoideae	<i>Abarema laeta</i> (Benth.) Barneby & J.W.Grimes		1	G	Tree	P		A.S. Maranho 6283
	<i>Anadenanthera</i> sp.	Fava branca	1	G		UN		
	<i>Enterolobium maximum</i> Ducke	Timbaúba	1	G	Tree	UN		A.S. Maranho 6193
	<i>Inga cylindrica</i> (Vell.) Mart.	Ingá cilíndrica	1	G	Tree	P		A.S. Maranho 6235
	<i>Inga</i> sp. 1	Ingá	1	G	Tree	UN		
	<i>Inga</i> sp. 2	Ingá ferro	16	G & U	Tree	UN		A.S. Maranho 6320
	<i>Inga</i> sp. 3	Ingá preta	4	G	Tree	UN		A.S. Maranho 6196
	<i>Inga</i> sp. 4	Ingá vermelha	40	G & U	Tree	UN		
	<i>Stryphnodendron guianense</i> (Aubl.) Benth.	Baginha	1	G	Tree	P		A.S. Maranho 6258
Lauraceae	<i>Endlicheria</i> sp.	Louro peludo	1	G	Tree	UN		A.S. Maranho 6221
	<i>Mezilaurus itauba</i> (Meisn.) Taub. ex Mez	Itaúba	2	U	Tree	LS	VU	A.S. Maranho 6303
	<i>Mezilaurus sprucei</i> (Meisn.) Taub. ex Mez	Louro itaúba	10	G & U	Tree	UN		A.S. Maranho 6212
	<i>Ocotea bofo</i> Kunth		1	U	Tree	LS		A.S. Maranho 6306
	<i>Ocotea oblonga</i> (Meisn.) Mez	Louro abacate	1	G	Tree	LS		A.S. Maranho 6297
	<i>Ocotea</i> sp. 1	Louro preto	8	G & U	Tree	UN		A.S. Maranho 6254
	<i>Ocotea</i> sp. 2	Louro	12	G & U	Tree	UN		A.S. Maranho 6317
Lecythidaceae	<i>Couratari guianensis</i> Aubl.	Tauari	20	G & U	Tree	LS	LC	A.S. Maranho 6234
	<i>Eschweilera coriacea</i> (DC.) S.A.Mori	Matá matá	5	G & U	Tree	LS		W. Castro 5329
	<i>Eschweilera truncata</i> A.C.Sm.	Matá matá preto	8	G & U	Tree	UN	LC	A.S. Maranho 6225
	<i>Gustavia augusta</i> L.	Castanharana	24	G & U	Tree	ES		A.S. Maranho 6253
Malvaceae	<i>Herrania nitida</i> (Poepp.) R.E.Schult.	Cacau jacaré	2	G	Tree	LS		A.S. Maranho 6279
	<i>Lueheopsis</i> sp.		1	U		UN		
	<i>Pseudobombax munguba</i> (Mart. & Zucc.) Dugand	Munguba	2	G	Tree	ES		A.S. Maranho 6207
	<i>Quararibea guianensis</i> Aubl.	Envira sapotinha	31	G & U	Tree	LS		A.S. Maranho 6267
	<i>Sterculia</i> sp.	Xixá	3	G & U	Tree	UN		A.S. Maranho 6244
	<i>Theobroma obovatum</i> Klotzsch ex Bernoulli	Cacaarana	22	G & U	Tree	UN		A.S. Maranho 6230
	<i>Theobroma</i> sp.	Cacau jacaré	1	U	Tree	UN		
	<i>Huberodendron swietenoides</i> (Gleason) Ducke		3	G & U	Tree	UN		A.S. Maranho 6213
Melastomataceae	<i>Miconia affinis</i> DC.	Buxixu	4	G & U	Shrub	P		A.S. Maranho 6259
	<i>Miconia</i> sp.	Buxixu	4	G		P		
	<i>Mouriri myrtifolia</i> Spruce ex Triana	Muriri	7	G	Tree	LS		A.S. Maranho 6216
	<i>Mouriri</i> sp.	Muriri	1	U	Tree	UN		
Meliaceae	<i>Carapa guianensis</i> Aubl.	Andiroba	1	U	Tree	LS		D.C. Daly 2450

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Table 1. Continued.

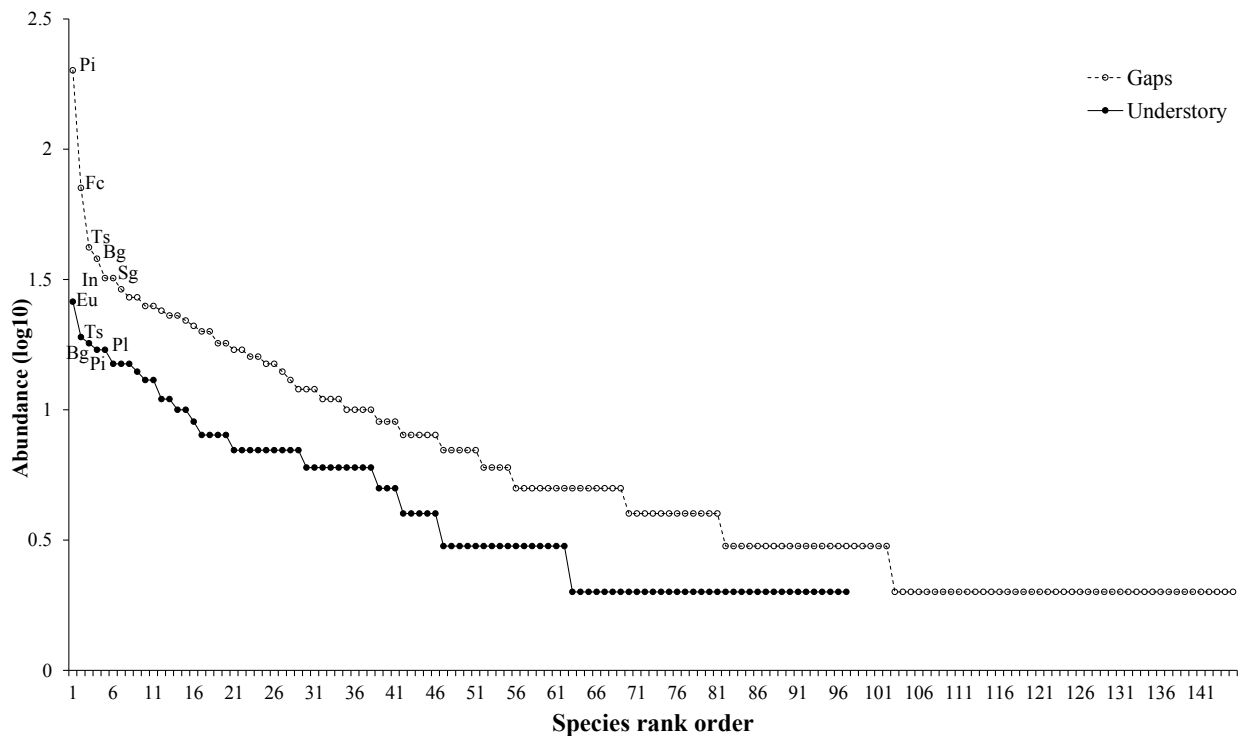
Family	Species	Common names	Abundance	Habitat <sup>1</sup>	Habit	Functional groups <sup>2</sup>	Threat status <sup>3</sup>	Voucher	
Moraceae	<i>Guarea</i> sp.	Jitô	42	G & U	Tree	UN		A.S. Maranho 6322	
	<i>Trichilia pleeana</i> (A.Juss.) C.DC.	Maraximbé	4	G & U	Tree	UN		A.S. Maranho 6247	
	<i>Brosimum alicastrum</i> Sw.	Inharé mole	2	U	Tree	LS		H. Medeiros 3957	
	<i>Brosimum guianense</i> (Aubl.) Huber	Inharé	54	G & U	Tree	ES		A.S. Maranho 6264	
	<i>Brosimum lactescens</i> (S.Moore) C.C.Berg	Manitê	7	G & U	Tree	LS	LC	A.S. Maranho 6224	
	<i>Castilla ullei</i> Warb.	Caucho	1	G	Tree	LS		H. Medeiros 3924	
	<i>Clarisia ilicifolia</i> (Spreng.) Lanj. & Rossberg	Janita	25	G & U	Tree	LS		A.S. Maranho 6276	
	<i>Clarisia racemosa</i> Ruiz & Pav.	Guariúba amarela	9	G & U	Tree	LS		A.S. Maranho 6239	
	<i>Naucleopsis glabra</i> Spruce ex Pittier	Muiratinga	13	G & U	Tree	UN		A.S. Maranho 6270	
	<i>Pereba mollis</i> (Poepp. & Endl.) Huber	Pama caucho	19	G & U	Tree	LS		A.S. Maranho 6268	
	<i>Pseudolmedia laevis</i> (Ruiz & Pav.) J.F.Macbr.	Pama	40	G & U	Tree	LS		A.S. Maranho 6323	
	<i>Pseudolmedia macrophylla</i> Trécul	Pama grande	2	G	Tree	LS		A.S. Maranho 6299	
	<i>Sorocea muriculata</i> Miq.		1	G	Tree	UN		A.S. Maranho 6192	
	<i>Sorocea</i> sp.	Jaca brava	32	G & U	Tree	UN		A.S. Maranho 6238	
	Myristicaceae	<i>Componeura ullei</i> Warb.	Ucuuba	8	G & U	Tree	UN		A.S. Maranho 6277
		<i>Iryanthera juruensis</i> Warb.	Ucuuba sangue de boi	3	G & U	Tree	LS		A.S. Maranho 6255
<i>Virola minutiflora</i> Ducke		Ucuuba	1	G	Tree	UN		A.S. Maranho 6257	
<i>Virola multinervia</i> Ducke		Ucuuba preta	7	G & U	Tree	UN		A.S. Maranho 6227	
<i>Virola</i> sp.		Ucuuba vermelha	1	G	Tree	UN		A.S. Maranho 6191	
<i>Eugenia acrensis</i> McVaugh		Araçá	2	G & U	Tree	LS		A.S. Maranho 6300	
<i>Eugenia</i> sp. 1		Araçá	1	G & U	Tree	UN			
<i>Eugenia</i> sp. 2		Araçá	51	G	Tree	UN		A.S. Maranho 6282	
<i>Neea floribunda</i> Poepp. & Endl.		João mole	36	G & U	Tree	ES		W. Castro 5676	
<i>Neea</i> sp. 1		João mole	2	G	Tree	UN			
<i>Neea</i> sp. 2		3	G & U	Tree	UN		A.S. Maranho 6217		
Olacaceae	<i>Aptandra tubicina</i> (Poepp.) Benth. ex Miers	Castanha de cotia	3	G & U	Tree	ES		A.S. Maranho 6226	
	<i>Chaunochiton kappleri</i> (Sagot ex Engl.) Ducke	Casca roxa	2	G	Tree	ES		A.S. Maranho 6195	
	<i>Heisteria duckei</i> Sleumer	Itaubarana	3	G & U	Tree	LS		A.S. Maranho 6263	
Piperaceae	<i>Minquartia guianensis</i> Aubl.	Aquariquara	3	G & U	Tree	LS		A.S. Maranho 6205	
	<i>Piper arboreum</i> Aubl.	Pimenta longa amarela	5	G	Shrub	P		L. Coêlho 14	
	<i>Piper hispidinervum</i> C.DC.	Pimenta longa amarela	7	G	Shrub	P		A.S. Maranho 6289	
	<i>Piper</i> sp. 1	Pimenta longa	216	G & U	Shrub	P		A.S. Maranho 6273	
	<i>Piper</i> sp. 2	Pimenta longa	15	G & U	Shrub	P		A.S. Maranho 6315	
	<i>Piper</i> sp. 3	Pimenta longa preta	5	G & U	Shrub	P		A.S. Maranho 6314	
	<i>Triplaris</i> sp.	Tachi preto	7	G	Tree	ES			
	<i>Cybianthus guyanensis</i> subsp. <i>pseudoicacoreus</i> (Miq.) Pipoly		1	G	Tree	UN		A.S. Maranho 6251	
	<i>Drypetes amazonica</i> Steyerm.		7	G & U	Tree	ES		A.S. Maranho 6308	
	<i>Alibertia claviflora</i> K.Schum.	Apuruí	3	G & U	Tree	UN		A.S. Maranho 6294	
Rubiaceae	<i>Alibertia</i> sp.		1	U	Tree	UN		A.S. Maranho 6309	
	<i>Alseis</i> sp.	Pau de remo	1	G	Tree	UN			

Continued

Table 1. Continued.

Family	Species	Common names	Abundance	Habitat <sup>1</sup>	Habit	Functional groups <sup>2</sup>	Threat status <sup>3</sup>	Voucher
	<i>Amaoua guianensis</i> Aubl.	Canela de veado	3	G & U	Tree	ES		A.S. Maranhão 6311
	<i>Capirona decorticans</i> Spruce	Mamaluco	4	G	Tree	ES		A.S. Maranhão 6262
	<i>Faramea capillipes</i> Müll. Arg.	Taboquinha	84	G & U	Tree	UN		A.S. Maranhão 6229
	<i>Palicourea</i> sp.		8	G	Tree	LS		A.S. Maranhão 6285
	<i>Psychotria hoffmannseggiana</i> (Willd. ex Schult.) Müll.Arg.		16	G & U	Shrub	UN		A.S. Maranhão 6197
	<i>Psychotria lupulina</i> Benth.		1	G	Shrub	UN		A.S. Maranhão 6190
	<i>Psychotria</i> sp. 1		16	G & U	Shrub	UN		
	<i>Psychotria</i> sp. 2	Chacrona	2	G	Shrub	UN		A.S. Maranhão 6201
	<i>Randia armata</i> (Sw.) DC.	Espinho de judeu	3	U	Shrub	ES		A.S. Maranhão 6288
	Indet. 4		3	G		UN		
Rutaceae	<i>Metrodorea flavida</i> K.Krause	Pirarara	2	G	Tree	LS		A.S. Maranhão 6261
Salicaceae	<i>Banara nitida</i> Spruce ex Benth.	Cabelo de cotia	2	G	Tree	ES		A.S. Maranhão 6194
	<i>Casearia gossypiosperma</i> Briq.	Laranjinha	5	G & U	Tree	ES	LC	A.S. Maranhão 6202
	<i>Lunania</i> sp. Hook.		1	U		UN		
Sapindaceae	<i>Allophylus pilosus</i> (J.F.Macbr.) A.H.Gentry	Vela branca	23	G & U	Tree	LS		A.S. Maranhão 6237
	<i>Talisia cerasina</i> (Benth.) Radlk.	Breu pitomba	6	G & U	Shrub	LS		A.S. Maranhão 6290
Sapotaceae	<i>Pouteria calmito</i> (Ruiz & Pav.) Radlk.	Abiu amarelo	17	G & U	Tree	LS		A.S. Maranhão 6272
	<i>Pouteria campanulata</i> Baehni	Abiurana ferrugem	2	G & U	Tree	LS		A.S. Maranhão 6204
	<i>Pouteria hispida</i> Eyma	Abiurana casca fina	10	G & U	Tree	LS		A.S. Maranhão 6291
	<i>Pouteria</i> sp. 1	Abiurana dura	3	G & U	Tree	UN		A.S. Maranhão 6298
	<i>Pouteria</i> sp. 2	Abiurana peluda	2	G & U	Tree	UN		
	<i>Pouteria</i> sp. 3	Abiu amarelo	1	U	Tree	UN		
	<i>Pradosia atrovioleacea</i> Ducke	Massarandubinha	8	G	Tree	UN	DD	A.S. Maranhão 6245
Siparunaceae	<i>Siparuna guianensis</i> Aubl.	Capitiú	36	G & U	Tree	ES		A.S. Maranhão 6274
Solanaceae	<i>Brunfelsia grandiflora</i> D.Don	Manacá	7	G & U	Shrub	UN		A.S. Maranhão 6241
Thymelaeaceae	<i>Schoenobiblus peruviana</i> Standl.	Envira seda	2	G	Tree	UN		A.S. Maranhão 6301
Ulmaceae	<i>Ampelocera</i> sp.	Envira iodo	10	G & U	Tree	UN		
Urticaceae	<i>Pourouma cecropifolia</i> Mart.	Torém	1	G	Tree	ES		A.S. Maranhão 6287
	<i>Pourouma guianensis</i> Aubl.	Torém	7	G	Tree	P		A.S. Maranhão 6292
	<i>Pourouma minor</i> Benoist	Torém mapati	20	G & U	Tree	ES		A.S. Maranhão 6275
	<i>Urena</i> sp.	Cansanção	2	G		UN		
Violaceae	<i>Amphirrhox</i> sp.	Fruto de macaco	38	G & U	Tree	UN		A.S. Maranhão 6271
	<i>Leonia glycyarpa</i> Ruiz & Pav.	Estalador	12	G & U	Tree	UN		A.S. Maranhão 6218
	<i>Rinoreaocarpus uler</i> (Melch.) Ducke		20	G & U	Tree	ES		A.S. Maranhão 6222
Vochysiaceae	<i>Qualea grandiflora</i> Mart.	Catuaba roxa	7	G & U	Tree	LS		A.S. Maranhão 6256

<sup>1</sup>Habitat: G = gaps and U = understory; <sup>2</sup>Functional groups: P = pioneers species, ES = early secondary species, LS = late secondary species, and UN = "unclassified"; <sup>3</sup>Status available only for the species present in the Brazilian Flora Red List, where: VU = vulnerable, LC = least concern, DD = data deficient.



**Figure 2.** Species abundance distribution curves (SAD) for gaps and understory. Pi=*Piper* sp.1; Fc=*Faramea capillipes*; Ts=*Tachigali setifera*; Bg=*Brosimum guianense*; In=*Inga* sp.4; Sg=*Siparuna guianensis*; Eu=*Eugenia* sp.2; Pl=*Pseudolmedia laevis*.

(Vogel), *Hymenaea parvifolia* Huber and *Mezilaurus itauba* (Meisn.) Taub. ex Mez) are commercially exploited in the Amazon, mainly for timber. Such a status for these species mean that more attention is needed when harvesting permits are granted from government.

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## LITERATURE CITED

- Acre. 2006. Zoneamento Ecológico-Econômico (ZEE) Fase II: documento síntese. Rio Branco: SEMA. 356 pp.
- Amaral, D.D. dos, I.C.G. Vieira, S.S. de Almeida, R. de P. Salomão, A.S.L. da Silva and M.A.G. Jardim. 2009. Checklist da flora arbórea de remanescentes florestais da região metropolitana de Belém e valor histórico dos fragmentos, Pará, Brasil. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 4(3): 231–289. <http://scielo.iec.pa.gov.br/pdf/bmpegcn/v4n3/v4n3a02.pdf>.
- APG 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(2): 105–121. doi: [10.1111/j.1095-8339.2009.00996.x](https://doi.org/10.1111/j.1095-8339.2009.00996.x)
- Bernardes, C. and F.R.C. Costa. 2011. Environmental variables and Piper assemblage composition: a mesoscale study in the Madeira-Purus interfluvium, Central Amazonia. *Biota Neotropica* 11(3): 83–91. doi: [10.1590/S1676-06032011000300006](https://doi.org/10.1590/S1676-06032011000300006)
- Brandani, A., G.S. Hartshorn and G.H. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *Journal of Tropical Ecology* 4(2): 99–119. doi: [10.1017/S0266467400002625](https://doi.org/10.1017/S0266467400002625)
- Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66(3): 682–687. doi: [10.2307/1940529](https://doi.org/10.2307/1940529)
- Brokaw, N.V.L. and S.M. Scheiner 1989. Species composition in gaps and structure of a tropical forest. *Ecology* 70(3): 538–541. doi: [10.2307/1940196](https://doi.org/10.2307/1940196)
- Budowski, G. 1965. Distribution of tropical American rain forest species in the light of successional processes. *Turrialba* 15(1): 40–42.
- Carvalho, A.L.de, B.W. Nelson, M.C. Bianchini, D. Plagnol, T.M. Kiplich and D.C. Daly. 2013. Bamboo-dominated forests of the southwest Amazon: detection, spatial extent, life cycle length and flowering waves. *PLoS One* 8(1): 1–13. doi: [10.1371/journal.pone.0054852](https://doi.org/10.1371/journal.pone.0054852)
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199(4335): 1302–1310. doi: [10.1126/science.199.4335.1302](https://doi.org/10.1126/science.199.4335.1302)
- Connell, J.H. and P.T. Green. 2000. Seedlings dynamics over thirty-two years in a tropical rain forest tree. *Ecology* 81(2): 568–584. doi: [10.2307/177449](https://doi.org/10.2307/177449)
- Daws, M.I., D.F.R.P. Burslem, L.M. Crabtree, P. Kirkman, C.E. Mullins and J.W. Dalling. 2002. Differences in seed germination responses may promote coexistence of four sympatric *Piper* species. *Functional Ecology* 16(2): 258–267. doi: [10.1046/j.1365-2435.2002.00615.x](https://doi.org/10.1046/j.1365-2435.2002.00615.x)
- Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12(2): 47–55. doi: [10.2307/2388156](https://doi.org/10.2307/2388156)
- Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18(1): 431–451. doi: [10.1146/annurev.es.18.110187.002243](https://doi.org/10.1146/annurev.es.18.110187.002243)



- Denslow, J.S., J.C. Schultz, P.M. Vitousek and B.R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71(1): 165–179. doi: [10.2307/1940257](https://doi.org/10.2307/1940257)
- Denslow, J.S. 1995. Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications*, 5(4): 962–968. doi: [10.2307/2269347](https://doi.org/10.2307/2269347)
- Dirzo, R. and P.H. Raven. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28: 137–167. doi: [10.1146/annurev.energy.28.050302.105532](https://doi.org/10.1146/annurev.energy.28.050302.105532)
- Duarte, A.F. 2006. Aspectos da climatologia do Acre, Brasil, com base no intervalo 1971–2000. *Revista Brasileira de Meteorologia* 21(3): 308–317. [http://rbmet.org.br/port/revista/revista\\_artigo.php?id\\_artigo=219](http://rbmet.org.br/port/revista/revista_artigo.php?id_artigo=219)
- Flora do Brasil 2020 em construção. 2016. Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. Accessed at <http://floradobrasil.jbrj.gov.br>, 20 March 2016.
- Fox, J.W. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution* 28(2): 86–92. doi: [10.1016/j.tree.2012.08.014](https://doi.org/10.1016/j.tree.2012.08.014)
- Gandolfi, S. 2000. História natural de uma floresta estacional semidecidual no município de Campinas (São Paulo, Brasil) [D.Sc. thesis]. Campinas: Universidade Estadual de Campinas. 551 pp.
- Gargiullo, M.B. Magnuson and L. Kimball. 2008. A field guide to plants of Costa Rica. New York: Oxford University Press. 542 pp.
- Griscom, B.W. and P.M.S. Ashton. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in southeastern Peru. *Forest Ecology and Management* 175(1–3): 445–454. doi: [10.1016/S0378-1127\(02\)00214-1](https://doi.org/10.1016/S0378-1127(02)00214-1)
- Griscom, B.W. and P.M.S. Ashton. 2006. A self-perpetuating bamboo disturbance cycle in a Neotropical forest. *Journal of Tropical Ecology* 22(5): 587–597. doi: [10.1017/S0266467406003361](https://doi.org/10.1017/S0266467406003361)
- Griscom, B.W., D.C. Daly and M.S. Ashton. 2007. Floristics of bamboo-dominated stands in lowland terra-firma forests of southwestern Amazonia. *Journal of the Torrey Botanical Society* 134(1): 108–125. doi: [10.3159/1095-5674\(2007\)134\[108:FOBSIL\]2.0.CO;2](https://doi.org/10.3159/1095-5674(2007)134[108:FOBSIL]2.0.CO;2)
- Hubbell, S.P., R.B. Foster, S.T. O'Brien, K.E. Harms, R. Condit, B. Weschler, S.J. Wright and S. Loo de Lao 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical Forest. *Science* 283(5401): 554–557. doi: [10.1126/science.283.5401.554](https://doi.org/10.1126/science.283.5401.554)
- Lorenzi, H. 2008. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Vol. 1. Nova Odessa: Instituto Plantarum, 368 pp.
- Lorenzi, H. 2009. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Vol. 2. Nova Odessa: Plantarum. 384 pp.
- Lorenzi, H. 2011. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Vol. 3. Nova Odessa: Plantarum. 384 pp.
- Magnusson, W.E., A.P. Lima, R. Luizão, F. Luizão, F.R.C. Costa, C.V. Castilho and V.F. Kinupp. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica* 5(2): 1–6. doi: [10.1590/S1676-06032005000300002](https://doi.org/10.1590/S1676-06032005000300002)
- Magurran, A.E. 2005. *Measuring biological diversity*. Oxford: Blackwell Science. 256 pp.
- Martinelli, G. and M.A. Moraes. 2013. *Livro vermelho da flora do Brasil*. Rio de Janeiro: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. 1100 pp.
- Matthews, T.J. and R.J. Whittaker. 2014. Fitting and comparing competing models of the species abundance distribution: assessment and prospect. *Frontiers of Biogeography* 6(2): 67–82. <https://escholarship.org/uc/item/3gz504j3>
- McGill, B.J., R.S. Etienne, J.S. Gray, D. Alonso, M.J. Anderson, H.K. Benecha, M. Dornelas, B.J. Enquist, B.J. Enquist, J.L. Green, F. He, A.H. Hulbert, A.E. Magurran, P.A. Marquet, B.A. Maurer, A. Ostling, C.U. Soykan, K.I. Ugland and E.P. White. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10(10): 995–1015. doi: [10.1111/j.1461-0248.2007.01094.x](https://doi.org/10.1111/j.1461-0248.2007.01094.x)
- Obiri, J.A.F. and M.J. Lawes. 2004. Chance versus determinism in canopy gap regeneration in coastal scarp forest in South Africa. *Journal of Vegetation Science* 15(4): 539–547. doi: [10.1111/j.1654-1103.2004.tb02293.x](https://doi.org/10.1111/j.1654-1103.2004.tb02293.x)
- Oliveira, L.S.B. 2011. Estudo do componente arbóreo e efeito de borda em fragmentos de Floresta Atlântica na Bacia Hidrográfica do Rio Tapacurá-PE [M.Sc. dissertation]. Recife: Universidade Federal Rural de Pernambuco. 92 pp.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed at <http://www.R-project.org>.
- Oksanen, J.F., G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens and H. Wagner. 2013. *Vegan: Community Ecology Package*. R package version 2.0-8. Accessed at <http://CRAN.R-project.org/package=vegan>.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62(4): 1041–1051. doi: [10.2307/1937003](https://doi.org/10.2307/1937003)
- Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. Portland: Department of Agriculture, Forest Service, Pacific Northwest Research Station. 44 pp.
- Santos, N.M.C. dos, Vale Júnior, J.F. do, R.I. Barbosa. 2013. Florística e estrutura arbórea de ilhas de mata em áreas de savana no norte da Amazônia brasileira. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 8(2): 205–221. [http://www.museu-goeldi.br/editora/bn/artigos/cnv8n2\\_2013/floristica%28santos%29.pdf](http://www.museu-goeldi.br/editora/bn/artigos/cnv8n2_2013/floristica%28santos%29.pdf)
- Schliemann, S.A. and J.G. Bockheim. 2011. Methods for studying treefall gaps: a review. *Forest Ecology and Management* 261(7): 1143–1151. doi: [10.1016/j.foreco.2011.01.011](https://doi.org/10.1016/j.foreco.2011.01.011)
- Sheil, D. and D.F.R.P. Burslem. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution* 18(1): 18–26. doi: [10.1016/S0169-5347\(02\)00005-8](https://doi.org/10.1016/S0169-5347(02)00005-8)
- Silva, I.B. 2011. Estrutura da comunidade vegetal e biomassa do estrato regenerativo em um fragmento florestal no sudoeste da Amazônia [M.Sc. dissertation]. Rio Branco: Universidade Federal do Acre. 54 pp.
- Silveira, M. 2005. A floresta aberta com bambu no sudoeste da Amazônia: padrões e processos em múltiplas escalas. Rio Branco: EDUFAC. 157 pp.
- Sousa, E. dos S., C.I. Salimon, R.L. Victoria, A. Krushe, S. Alin, N.K. Leite. 2008. Dissolved inorganic carbon and pCO<sub>2</sub> in two small streams draining different soil types in Southwestern Amazonia, Brazil. *Revista Ambiente & Água* 3(2): 37–50. doi: [10.4136/ambiente.51](https://doi.org/10.4136/ambiente.51)
- Steege, H., N.C.A. Pitman, D. Sabatier, C. Baraloto, R.P. Salomão, J.E. Guevara, et al. 2013. Hyperdominance in the Amazonian tree flora. *Science* 342(6156): 325–342. doi: [10.1126/science.1243092](https://doi.org/10.1126/science.1243092)
- Torezan, J.M.D. and M. Silveira. 2000. The biomass of bamboo (*Guadua weberbaueri* Pilger) in open forest of the southwestern amazon. *Ecotropica* 6(1): 71–76.

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