



# Patterns of floristic diversity and composition in floodplain forests across four Southern Amazon river tributaries, Brazil

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## ARTICLE INFO

### Article history:

Received 22 November 2016

Received in revised form 9 February 2017

Accepted 15 February 2017

Edited by Karsten Wesche

Available online 20 February 2017

### Keywords:

Amazonia

Floristic diversity

Floodplain forest

Paleo-várzea

Tree species composition

Tree inventory

Várzea

## ABSTRACT

Floodplain forests cover extensive areas of the Amazon basin, but the number of tree inventories is low. Vast floodplain regions therefore remain floristically unknown. We present a quantitative inventory of floodplain forests from four Amazon river basins (Jutaí, Juruá, Tefé and Purus), investigate within- and between-basin floristic similarity, and examine patterns of tree species dominance and distribution. Twelve hectares with all trees  $\geq 10$  cm dbh were inventoried; three hectares in each river basin. Rarefaction curves were used to compare species richness across study areas. GNMDS was used to investigate within- and between-basin floristic similarity, combined with an analysis of similarity (ANOSIM) to test for significant differences. In total, 7722 stems representing 518 species were recorded. Inventory plots from the same river basin were clearly clustered in the GNMDS ordination and the ANOSIM showed that floristic composition differed significantly both between and within study areas. Fabaceae was the most abundant family and *Eschweilera albiflora* the most abundant species. Only nine species were highly abundant in more than one study area, whereas 220 species were recorded in only one sample plot. Our results demonstrate high levels of beta-diversity in Amazonian floodplain forests. The high number of uncommon species is consistent with other studies.

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## 1. Introduction

Floodplains subjected to long-lasting and monomodal flood pulses cover approximately 760,000 km<sup>2</sup> along the Amazon River and its larger tributaries (Melack and Hess, 2010; Junk et al., 2011). Forests occurring on these vast floodplains might endure inundation up to 230 days per year, as the pronounced periodicity of precipitation, the Andean snow melt and the low declivity of the basin, combine to cause seasonal floods that may reach 10–15 m in amplitude in central Amazonia (Junk, 1989; Wittmann et al., 2004). Many adaptations have been described for plant species that inhabit these environments. They include reductions in photosynthetic activity and growth during flooding (Worbes et al., 1992; Worbes, 1997; Parolin, 2000), anaerobic metabolism (Fernandes-Corrêa and Furch, 1992; Schlüter et al., 1993), adventitious roots

(Parolin, 2001), and hydrochoric and ichthyochoric dispersal strategies (Kubitzki and Ziburski, 1994; Lopez, 2001).

Amazonian floodplains were recently re-classified by Junk et al. (2011) as (i) floodplains of high fertility (white-water river floodplains, or várzea), (ii) floodplains of low fertility (black- or clear-water river floodplains, or igapó) and (iii) floodplains of intermediate fertility (black-water river floodplains on paleo-whitewater substrates, or floodplain paleo-várzea). Várzea floodplains are the most extensive and cover approximately 275,000 km<sup>2</sup> (Junk et al., 2011). Their rivers carry large amounts of nutrient-rich Tertiary/Quaternary sediments originating from the Andes or pre-Andean regions. Igapó covers an area of approximately 180,000 km<sup>2</sup> (Melack and Hess, 2010) and occurs along rivers that carry small amounts of ancient Precambrian sediments originating from the Guyana and Central Brazilian Shields. Floodplain paleo-várzeas cover at least 125,000 km<sup>2</sup> and occur on fluvial Andean deposits that have been abandoned by white-water rivers. These floodplains are inundated by small to intermediate black-water rivers that originate in cratonic areas and carry these already once-deposited paleo-sediments (Junk et al., 2011).

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The floristic composition of some Amazonian floodplain forests was described at the beginning of the last century by researchers such as Spruce (1908), Huber (1906, 1910) and Ducke (1913). However, the number of tree inventories in floodplain forest is approximately four times lower than in Amazonian upland forests (hereafter, terra firme; ter Steege et al., 2013). Most floodplain inventories have focused on várzea forest where approximately 100 ha have been inventoried in total (summarized in ter Steege et al., 2013). In igapó and paleo-várzea forest, only about 30 ha of inventories are currently available (e.g. Keel and Prance, 1979; Campbell et al., 1986; Ayres, 1993; Ferreira and Prance, 1998; Haugaasen and Peres, 2006; Montero et al., 2012). These inventories are mainly concentrated along the Amazon river, in the Caquetá/Japurá floodplains or in the Madeira river headwaters (ter Steege et al., 2013). Vast Amazonian floodplain regions therefore remain poorly known floristically (Parolin et al., 2004; Schulman et al., 2007).

It has been shown that tree species diversity and composition vary substantially between and within floodplain types in Amazonia (Worbes et al., 1992; Ayres, 1993; Ferreira and Stohlgren, 1999; Ferreira, 2000; Albernaz et al., 2012; Assis and Wittmann, 2011). Várzea forest generally supports a higher number of species than igapó, and is recognized as the most species-rich floodplain forest worldwide (Wittmann et al., 2006, 2010). High habitat diversity, caused by an extremely dynamic environment and high substrate fertility may promote and sustain this high species richness (e.g. Kalliola et al., 1991; Wittmann et al., 2002, 2004). Habitat heterogeneity has also been indicated as the main driver of the high beta-diversity at a local scale in várzea, while geographic gradients coupled with differences in flooding regimes and substrate fertility appear to be more important at larger scales across the Amazon floodplains (Wittmann et al., 2010; Assis et al., 2015a).

In this paper, we present a quantitative floristic inventory of várzea and paleo-várzea forests located along four Amazon river tributaries of central-western Brazilian Amazonia where little or no previous systematic botanical collections have been implemented. More specifically, we address the following questions: (i) How does tree diversity vary at local and regional scales in Amazonian floodplain forests containing different substrate conditions? (ii) Do floodplain forests with different historic-geographic origins, but situated within the same geographic area, support distinct tree assemblages? (iii) What are the patterns of tree species dominance and distribution at a regional scale? We discuss our results in light of previous floristic inventories across Amazonian floodplain forests.

## 2. Methodology

### 2.1. Study areas

Tree inventories were carried out in four central-western Amazonian floodplain forests located along different tributaries of the Solimões (=Amazon) river: Purus (S4°19'; W61°52'), Tefé (S4°9'; W65°6'), Juruá (S3°14'; W66°3') and Jutai (S3°22'; W67°28'; Fig. 1). All study areas are located in the lower reaches (in proximity to the confluence with the Amazon river) of each river basin and thus situated at similar latitude, but are separated longitudinally by a minimum and maximum distance of approximately 120 and 600 km, respectively. The Purus and Juruá rivers are white-water rivers carrying large amounts of nutrient-rich sediments from the Andes. Floodplains along these rivers are thus classed as várzea. The Tefé and Jutai rivers carry paleo-sediments originating from the Andes, and are therefore classed as floodplain paleo-várzeas (Junk et al., 2011).

All four study areas are subjected to a predictable, long-lasting (>5 months), monomodal flood pulse (Fig. 2). Tefé, Juruá and Jutai

experience the flooding peak in April/May and Purus in June. October is the month in which all study areas have the lowest river level. The Purus has the highest flood amplitude, followed by Juruá, Jutai and Tefé (Fig. 1). The Purus also has the highest flooding average (days/year<sup>-1</sup>) at 128.3 ± 56.6 days, followed by Jutai (120.4 ± 38.5), Juruá (114 ± 22.4) and Tefé (97.5 ± 58.5), respectively. Annual rainfall is approximately 2700, 2800, 2600 and 2500 mm, for Juruá, Jutai, Purus and Tefé, respectively. None of the study areas have more than one month per year with rainfall <100 mm (Sombroek, 2001).

### 2.2. Forest inventory

Tree inventories were conducted during the 2009 and 2010 low-water season. In total, 12 ha of floodplain forest were inventoried; three hectares in each river basin. All plots were placed in late-successional forest located far from cities and major settlements (at least 50 km). We therefore considered the forests pristine. Due to floodplain heterogeneity, inventory plots ranged from 0.25–1.0 ha (mean = 0.43 ± 0.15 sd)

Distance between plots within the same basin ranged from 0.5 to 10 km (mean = 4.71 ± 2.31 sd). Details of size and geographic coordinates of the sample plots are presented in the supplementary information (Table S1). All trees ≥10 cm in diameter at breast height (dbh) within each plot were individually tagged and had their dbh measured. Non-timber species (e.g. lianas, epiphytes or hemi-epiphytes) were not included in the inventories. Vouchers were collected from all trees and transported to the herbarium at the National Institute of Amazonian Research (INPA), Manaus, where they were identified to the lowest taxonomic level possible. Specimens not identified to species were assigned to morpho-species. Conforming to herbarium regulations, only fertile material was permanently deposited.

### 2.3. Data analysis

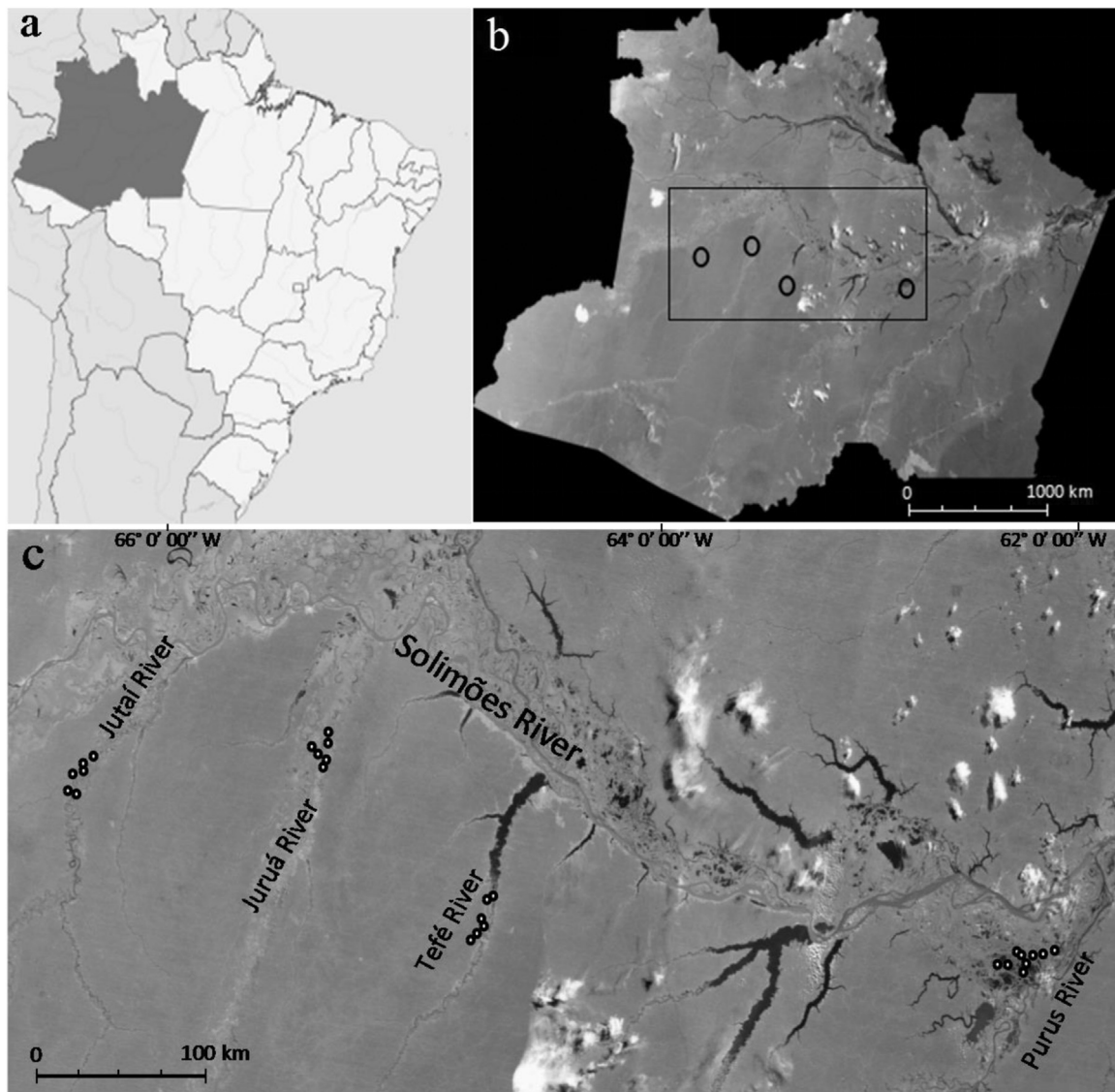
To investigate patterns of floristic composition we calculated relative abundance (RA), relative frequency (RF), relative dominance (based on basal area) (RD) and importance value index (IVI; Curtis and McIntosh, 1951) for each species in each study area. The family importance value (FIV; Mori et al., 1983) was also calculated for each family. Alpha-diversity was derived using the Fisher's Alpha Index (Fisher et al., 1943) and differences between study areas were tested using Mann-Whitney *U* tests. Differences were considered significant when  $p < 0.01$ .

In order to remove potential effects of different inventory plot sizes, rarefaction curves were used to compare species richness across study areas. Global Non-metric Multidimensional Scaling (GNMDS; Minchin, 1987) with Bray-Curtis distance measure based on 100 iterations was used to investigate within- and between-basin floristic similarity. An analysis of similarity (ANOSIM) was performed to examine significant differences in species composition between and within study areas. This analysis also uses the Bray-Curtis distances and includes a nonparametric permutations test equivalent to an ANOVA for similarity matrices (Clarke, 1993). All analyses were performed in R version 2.14.1 (R Development Core Team 2011), using the Vegan package (Oksanen, 2005).

## 3. Results

### 3.1. Species diversity

A total of 7722 stems representing 518 species (of which 211 are morpho-species), 203 genera and 55 families were recorded in the 12 ha inventoried. The Jutai supported the highest number of individuals, but Purus contained the highest number of species



**Fig. 1.** (a) Map of Brazil divided into geopolitical zones (black lines) and the State of Amazonas shown in gray. (b) State of Amazonas and the river basins included in the study (black circles inside the rectangle). (c) Location of the individual inventory plots within each river basin. Image credits: Brasil Visto do Espaço (2012), In: Miranda, E.E., Coutinho, A.C., (Eds.), Embrapa, Campinas (Brazil).

**Table 1**

Number of plant individuals, families, genera and species for each of the river basins inventoried.

Study area	Individuals	Families	Genera	Species
Jutai	2245	41	119	146
Juruá	1846	41	112	146
Tefé	1750	46	125	192
Purus	1881	47	122	213
Total	7722	55	203	518

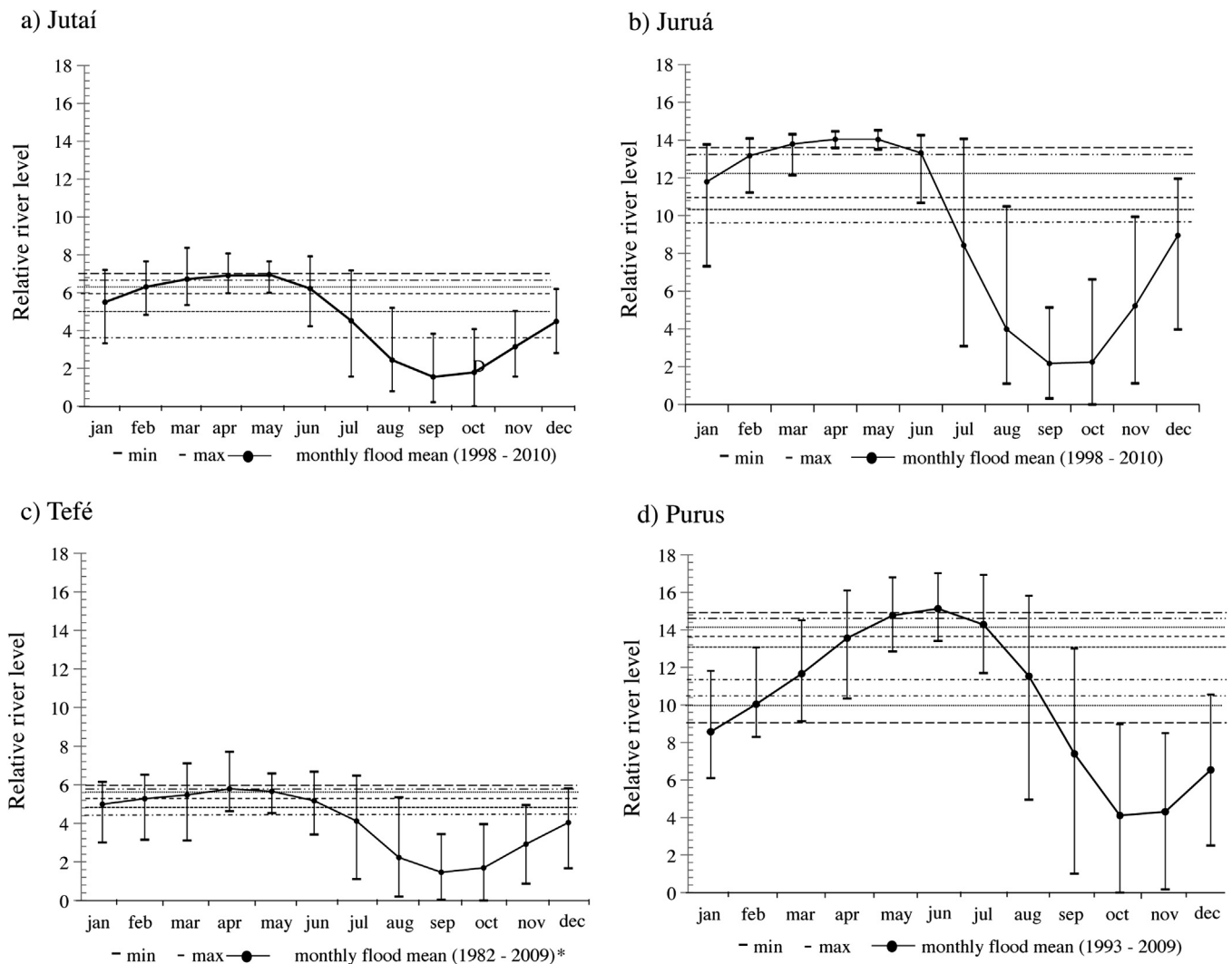
(Table 1). The Purus had the highest number of morpho-species (25% of all individuals sampled), followed by the Tefé (19%), Juruá (15%) and Jutai (11%). A complete list of tree species recorded is provided in Appendix A.

The highest Fisher's alpha values were obtained in the Tefé and the lowest in the Jutai (Fig. 3). However, no significant difference in Fisher's alpha values was observed between study areas (Fig. 3). The slope of the species rarefaction curves typically declined as sample sizes increased for all study areas, but an asymptote could not be fully reached for the Purus or the Tefé (Fig. 4).

### 3.2. Floristic composition

Inventory plots from the same river basin were clearly clustered in the GNMDS ordination (Fig. 5), showing that species composition and abundance was more similar to plots from the same river basin than to plots from other basins. The ANOSIM showed that floristic composition differed not only within all study areas (Juruá:  $R=0.695$ ,  $p=0.001$ ; Jutai:  $R=0.898$ ;  $p=0.001$ ; Purus:  $R=0.931$ ,  $p=0.001$ ; Tefé:  $R=0.774$ ,  $p=0.001$ ), but also between study areas (supplementary material Fig. S1). The Purus had the highest dissimilarity to all other study areas. The variation in species composition between plots within the Purus basin was also highest among study areas, whereas Juruá plots were most similar (Table 2).

Across study areas, Jutai and Tefé shared the highest number of species, but only attained a similarity value of around 14% (Table 2). In fact, the number of species exclusive to each study area was considerable, with 152 (78%) in the Purus, 116 (60%) in the Tefé, 72 (49%) in the Juruá and 63 (43%) in the Jutai. Only fourteen species (2% of all species sampled) occurred across all four study areas.



**Fig. 2.** Average monthly relative river level (solid black line) with maximum and minimum levels (bars) of the Jutai (a), Juruá (b), Tefé (c) and Purus (d) rivers. Topographic level of each sample plot is presented in the horizontal dashed lines. Data are based on the flood mark on the tree trunks resulting from the last high-water period, coupled with historical river level data from water gauges of the Brazil's Agência Nacional de Águas (ANA; <http://hidroweb.ana.gov.br>). For further details of this methodology see Wittmann and Junk (2003) and Schongart et al. (2005). Star (\*) represents data absent for the period 1990/1991.

**Table 2**

Bray-Curtis similarity (bold) between tree species assemblages within and across the four river basins, including the number and percentage of shared species (italic).

	Jutai	Juruá	Tefé	Purus
Jutai	<b>0.294</b>	<b>0.134</b>	<b>0.142</b>	<b>0.046</b>
Juruá	46 (18.7%)	<b>0.377</b>	<b>0.108</b>	<b>0.074</b>
Tefé	61 (21.9%)	42 (14.1%)	<b>0.319</b>	<b>0.044</b>
Purus	35 (10.8%)	42 (13.3%)	30 (8%)	<b>0.13</b>

### 3.3. Species dominance and distribution

The 10 most abundant families comprised 68% of all tree species sampled. Fabaceae had the highest number of individuals across the four study areas (15%), followed by Euphorbiaceae (10%), Lecythidaceae (8%), and Annonaceae (7%). Fabaceae was the most abundant family in Juruá, Jutai and Tefé, whereas Malvaceae was the most abundant in the Purus. The high abundance of Malvaceae in the Purus is due to a large number of individuals of *Luehea cymulosa* and *Pseudobombax munguba*. These results are mirrored by the Family Importance Value (FIV), which shows that Fabaceae was the most important family in Juruá, Jutai and Tefé, and Malvaceae in the Purus (Table 3). Family dominance was highest in the Juruá, where

the 10 most important families comprised more than 70% of the total FIV, and lowest in the Purus (62%; Table 3).

*Eschweilera albiflora* was the most abundant tree species across the four study areas, followed by *Virola surinamensis*, *Pterocarpus rohrii* and *Pseudobombax munguba*. *Virola surinamensis* occurred in the highest number of sample plots (18; 67% of the total number of plots sampled), followed by *Eschweilera albiflora* and *Vatairea guianensis* (17; 63% for both species). In contrast, a high number of species (220; 42% of total number of species sampled) were recorded in only one sample plot and 369 species (71%) had less than one tree per hectare on average. In total, 114 (22%) species were represented by a single tree. The Purus had the highest number of singletons (64; 30%), followed by Jutai (30; 20%), Juruá (39; 20%) and Tefé (22; 15%).

*Virola surinamensis* was the most important tree species in the Juruá (Table 4a). This is a reflection of its large stems, allowing this species to dominate the basal area of the Juruá sample despite its low abundance. Purus and Tefé were the only study areas where palm species (*Astrocaryum jauari* and *Euterpe precatoria*) were among the 10 most important species (Table 4c and d). Two species in the Jutai, *Brosimum lactescens* and *Eschweilera albiflora*, predominated and together presented one-sixth of the total

**Table 3**  
Ten most important families, listed in descending order of family importance value (FIV), at four southern tributaries of the Solimões (=Amazon) river, central Amazonia, Brazil. The FIV value provided in the light gray row is the sum of the 10 most important families in each tributary; the dark gray row presents the summed FIV for the remaining families in each river basin.

Jutaí		Juruá		Tefé		Purus	
Family	FIV (%)	Family	FIV (%)	Family	FIV (%)	Family	FIV (%)
Fabaceae	16.8	Fabaceae	16.8	Fabaceae	18.9	Malvaceae	13.3
Euphorbiaceae	10.2	Malvaceae	9.3	Lecythidaceae	11.2	Fabaceae	11.1
Lecythidaceae	9.4	Euphorbiaceae	8.7	Chrysobalanaceae	8.7	Euphorbiaceae	6.8
Sapotaceae	7.1	Annonaceae	8.6	Sapotaceae	6.2	Sapotaceae	6.5
Moraceae	6.4	Myristicaceae	7.5	Annonaceae	5.1	Annonaceae	5.5
Annonaceae	5.5	Lecythidaceae	5.3	Moraceae	5.1	Bignoniaceae	4.1
Lauraceae	4.7	Sapotaceae	4.7	Euphorbiaceae	4.2	Myrtaceae	4
Chrysobalanaceae	4.2	Violaceae	14	Clusiaceae	4.1	Moraceae	3.9
Myristicaceae	3.1	Apocynaceae	3.3	Myrtaceae	3.6	Lauraceae	3.4
Malvaceae	2.5	Lauraceae	3.2	Lauraceae	3.5	Myristicaceae	3.2
Σ 1-10	70.1	Σ 1-10	72.8	Σ 1-10	70.9	Σ 1-10	61.8
Σ 11-41	29.9	Σ 11-41	27.2	Σ 11-46	29.1	Σ 11-47	38.2

**Table 4**  
Relative abundance (RA), relative frequency (RF), relative dominance (RD), and importance value index (IVI) of the ten most important species at four southern tributaries of the Solimões (=Amazon) river, central Amazonia, Brazil. Species are listed in descending order of IVI. The IVI value provided in the light gray row is the sum of the 10 most important species in each tributary; the dark gray row presents the summed IVI for the remaining species in each river basin.

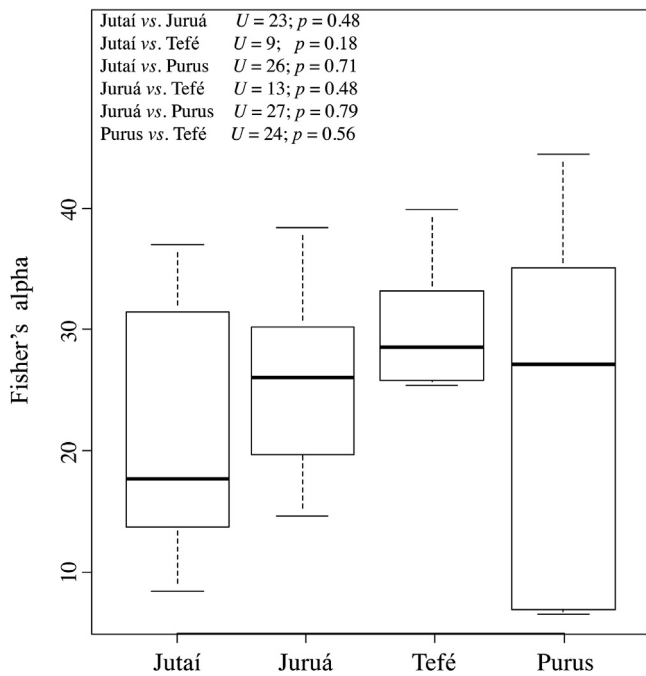
a. Jutaí					b. Juruá				
Species	RA	RF	RD	IVI (%)	Species	RA	RF	RD	IVI (%)
1 <i>Brosimum lactescens</i>	4.8	2.5	18.4	8.6	<i>Virola surinamensis</i>	7.4	3.6	10.2	7
2 <i>Eschweilera albiflora</i>	4.7	3.1	15.7	7.8	<i>Leonia crassa</i>	8	3.6	6.1	5.9
3 <i>Mabea nitida</i>	6.7	3.1	8	5.9	<i>Campsiandra angustifolia</i>	2	1.75	9.5	4.5
4 <i>Eschweilera ovalifolia</i>	4.1	3	10.4	5.8	<i>Lueheopsis rosea</i>	1.8	1.9	8.9	4.2
5 <i>Oxandra polyantha</i>	5.1	3.4	4.7	4.4	<i>Pterocarpus rohrii</i>	4.2	3.5	3.2	3.7
6 <i>Pterocarpus rohrii</i>	4.4	2.7	4.1	3.8	<i>Quararibea guianensis</i>	4.2	2.5	2.9	3.2
7 <i>Maclobium acaciifolium</i>	2.6	1.4	5.3	3.1	<i>Eschweilera ovalifolia</i>	2.4	1.9	3.7	2.7
8 <i>Hevea brasiliensis</i>	2.7	1.9	3.3	2.7	<i>Hevea brasiliensis</i>	2.7	2.7	1.6	2.4
9 <i>Pseudoxandra polyphleba</i>	2.6	2.3	1.7	2.2	<i>Malouetia tamaquarina</i>	2.7	2.6	1.3	2.2
10 <i>Pouteria sp. 6</i>	1.9	2.3	2.3	2.2	<i>Sapium sp. 2</i>	2.4	2	2	2.1
Σ 1-10	39.6	25.9	74.2	46.5	Σ 1-10	38.1	26.3	49.5	37.9
Σ 11-146	60.3	74.1	25.7	53.5	Σ 11-146	61.9	73.7	50.6	62.1

c. Tefé					d. Purus				
Species	RA	RF	RD	IVI (%)	Species	RA	RF	RD	IVI (%)
1 <i>Eschweilera albiflora</i>	7.7	3.7	11.6	7.7	<i>Pseudobombax munguba</i>	7.9	1.8	12.4	7.5
2 <i>Licania sp. 1</i>	3.8	2.9	3.7	3.5	<i>Tabebuia barbata</i>	7.7	2.3	6.6	5.6
3 <i>Euterpe precatoria</i>	5.7	2.4	2	3.4	<i>Luehea cymulosa</i>	5.7	0.8	5.7	4.2
4 <i>Maclobium angustifolium</i>	2.6	2.3	2.9	2.6	<i>Astrocaryum jauari</i>	0.7	0.6	10.6	4
5 <i>Hevea brasiliensis</i>	2	2.3	3.1	2.5	<i>Piranhea trifoliata</i>	2.8	1.7	3.3	2.7
6 <i>Tapura juruana</i>	2	1.6	3	2.2	<i>Pouteria elegans</i>	4.6	1.1	1.3	2.4
7 <i>Swartzia sp. 1</i>	2	1.7	2.9	2.2	<i>Virola surinamensis</i>	2.5	1.9	2.6	2.4
8 <i>Virola surinamensis</i>	1.9	1.6	3	2.2	<i>Vitex cymosa</i>	2.6	1.1	2.1	2
9 <i>Lecythis prancei</i>	2.6	2.1	1.7	2.1	<i>Mabea sp.</i>	2.9	1.9	1	1.5
10 <i>Guatteria sp. 1</i>	1.9	1.7	2.1	2	<i>Himatanthus sucuuba</i>	1.7	1.6	1.2	1.5
Σ 1-10	32.5	22.5	36.2	30.4	Σ 1-10	39.3	15	47.1	33.8
Σ 11-192	67.5	77.5	63.8	69.6	Σ 11-213	60.6	85	52.9	66.2

IVI (Table 4b). In fact, species dominance was highest in the Jutaí where the ten most important species accounted for almost half of the total IVI (46%), whereas Tefé had the lowest species dominance with 30.4%. The ten most important species comprised 38% and 34% of the IVI in Juruá and Purus, respectively. Only four species (*E. albiflora*, *H. brasiliensis*, *P. rohrii* and *V. surinamensis*) featured among the 10 most important species in all study areas (Table 4a–d).

In terms of abundance, sixteen species accounted for 50% of all individual trees in both Juruá and Purus (11% and 7% of all species sampled, respectively). In the Jutaí and Tefé, 50% of all individuals was represented by 15 (10%) and 22 (11%) species, respectively. Only nine species were highly abundant in more than one study area, with *E. albiflora*, *H. brasiliensis* and *V. surinamensis* dominating abundance across three study areas (Jutaí, Juruá and Tefé).

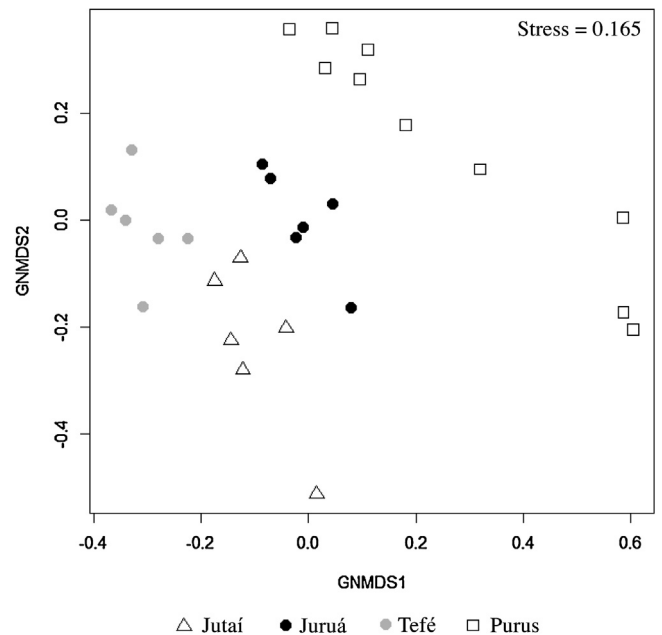


**Fig. 3.** Mean ( $\pm$ sd) Fisher's Alpha coefficient for floristic inventory plots in Jutai, Juruá, Tefé and Purus, central-western Amazonia, Brazil. Mann-Whitney *U*-test results for all comparisons between study areas are presented in the figure.

#### 4. Discussion

##### 4.1. Species diversity

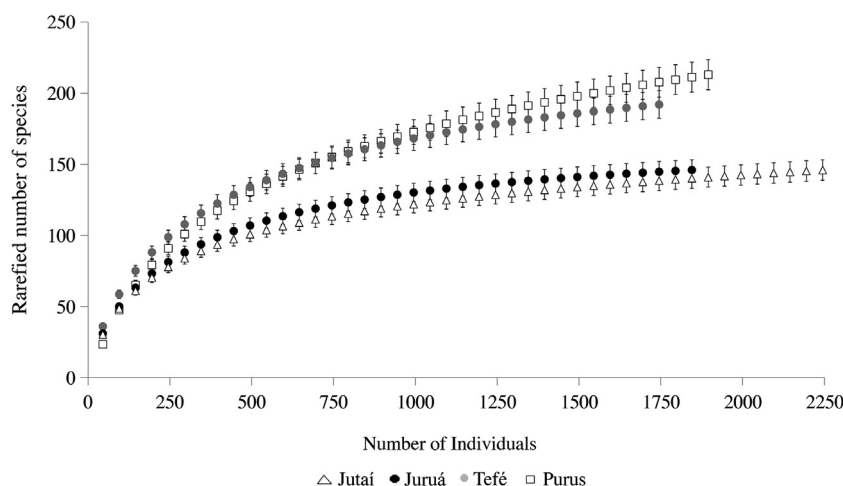
Fisher's alpha-diversity values did not differ significantly between study areas and values obtained were similar to the majority of other várzea forest inventories (see Wittmann et al., 2006). Nevertheless, the Tefé plots had the highest mean alpha diversity in our study. This is somewhat surprising given that this is a paleo-várzea forest and thus occurs on substrates that are more nutrient poor than várzea. A positive correlation between substrate fertility and tree alpha-diversity is well established on Amazonian floodplains (Prance, 1979; Kubitzki, 1989; Duque et al., 2002; Haugaasen and Peres, 2006; Wittmann et al., 2006; Dexter et al., 2012). There may be several reasons for our findings. First, the Tefé floodplain forests endure a shorter inundation period than the other study areas. It is therefore possible that these forests harbour tree species from surrounding upland forest capable of surviving shorter peri-



**Fig. 5.** Global non-metric multidimensional scaling (GNMDS) ordination of 28 floristic inventory plots from the Jutai, Juruá, Tefé and Purus river basins, central-western Amazonia Brazil. Plots are distributed in ordination space based on Bray-Curtis distances.

ods of water-logging. Secondly, this region is estimated to have one of the highest terra firme tree alpha-diversities in the entire Amazon basin (ter Steege et al., 2003). Kubitzki (1989) stated that many floodplain tree species are ecotypes originating from surrounding terra firme. The Tefé floodplain alpha-diversity values may therefore reflect the high diversity in adjacent terra firme. Third, a recent study shows that paleo-várzea may be a transition phase between várzea and igapó, and that high alpha-diversity values in paleo-várzea are due to the coexistence of species typical of várzea and igapó (Assis et al., 2015b).

The Jutai had the lowest alpha-diversity levels despite having the highest tree density. Although a positive correlation between tree density and tree diversity has been reported for terra firme forests (Condit et al., 1996; ter Steege et al., 2003), this relationship does not hold for Amazonian floodplains where an opposite pattern has been established for both igapó (Ferreira, 1997; Montero et al., 2012) and várzea (Campbell et al., 1992; Wittmann et al., 2004) forests. Our results thus corroborate earlier findings.



**Fig. 4.** Rarefied number of species accumulated per 50 individuals for each study area. Standard error is presented as vertical bars.

#### 4.2. Floristic composition

Tree species composition differed significantly both within and between study areas, demonstrating high levels of beta-diversity in Amazonian floodplain forests. Small-scale changes to environmental conditions have been linked to species occurrences and distribution across the Amazonian forest landscape (e.g. Hubbell and Foster, 1986; Gentry and Ortiz, 1993; Tuomisto and Ruokolainen, 1994; Wittmann et al., 2010). The dynamic nature of Amazonian floodplains, particularly várzeas, and differences in flood regimes, may create a patch-work of habitats that could significantly influence beta-diversity. However, we only sampled late-successional forest. An even higher species turnover within study areas would be expected if the entire successional gradient had been sampled.

Sample plots within the same study area were floristically more similar to each other than plots from different study areas. Yet, the two paleo-várzea forests sampled (Jutaí and Tefé) were floristically more similar to each other than to the two várzea forests, despite being far (>250 km) apart. These results suggest that historic and environmental variables may significantly influence species turnover. In this context, flooding regime, substrate characteristics and geographic variables have previously been recognized as important in shaping tree assemblages across sites (e.g. Prance 1979; Balslev et al., 1987; Kubitzki, 1989; Worbes et al., 1992; Terborgh and Andresen, 1998; Duque et al., 2002; Haugaasen and Peres, 2006; Wittmann et al., 2006; Albernaz et al., 2012; Assis et al., 2015a). At the same time, our results indicate low connectivity (high geographic isolation) between river basins – even though a large number of floodplain tree species are dispersed by water or fish (Goulding 1983).

#### 4.3. Dominance and distribution

Family composition in the floodplain forests inventoried is similar to that recorded elsewhere. For example, Fabaceae was the most important family across our study areas. This is in agreement with other studies conducted in Amazonian floodplain (e.g. Ayres, 1993; Keel and Prance, 1979; Ferreira, 1997; Haugaasen and Peres, 2006; Wittmann et al., 2010) and terra firme (Gentry, 1988, 1992; Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006) forest, underlining the importance of this family in Neotropical forests. The exception was the Purus, where Malvaceae was the most important family. Malvaceae contains several species (e.g. *P. munguba* and *L. cymulosa*), which are known to occur at higher abundances in early successional stages of várzea forest (Wittmann et al., 2006, 2010). Since we only inventoried late-successional forest, it appears that the highly dynamic nature of várzea floodplains (erosion and deposition of sediments) allows the existence of these species also within late-successional forests – probably through elevated rates of disturbance events, such as tree falls, related to hydraulic changes and small-scale differences in sediment deposition and erosion. In paleo-várzea such processes are much reduced. The fact that Malvaceae is the second most important family in várzea forests of the Juruá and that several species of this family are among the most important for these two várzea areas (Purus and Juruá), but are almost absent from our paleo-várzea sites (Jutaí and Tefé), supports this assessment. Lecythidaceae on the other hand was more important in the paleo-várzeas of the Juruá and Tefé. This may be connected to substrate fertility. Previous studies show that the abundance of Lecythidaceae is positively correlated with more nutrient-poor substrates across the Amazon (Mori et al., 2001; Coronado et al., 2009; Montero et al., 2012).

All study areas were dominated by a few abundant species. Thirty-eight species (7% of 518 species) accounted for 50% of the total number of stems recorded in the four study areas. Twenty-

four of these species were recently classed as “hyperdominant” in Amazonian forests (ter Steege et al., 2013). For example, the palm *Euterpe precatoria* was among the 10 most important species in the Tefé and is the most dominant species among all hyper-dominant species in the basin (ter Steege et al., 2013). The high abundance of this palm species and the *Astrocaryum jauari* palm in the Purus is therefore likely to be a natural phenomenon. Several other studies report similar results, where a large number of trees belonging to a small set of common species form predictable oligarchies that dominate large areas of forest (Pitman et al., 2001; Terborgh et al., 2002; ter Steege et al., 2013).

In contrast, many species in our sample were uncommon. This is also consistent with other local- and continent-scale studies from the Amazon (e.g. ter Steege et al., 2013; Pitman et al., 1999). The majority of these species are reported to occur at low densities in other várzea or paleo-várzea inventories (summarized Wittmann et al., 2006). In fact, around 90% of the species (not including morpho-species) recorded in the current study have been registered in other floodplain forests, even though the number of species restricted to a single study area was considerable (range 43–78%). Our data therefore substantiate findings by Wittmann et al. (2013), who suggest that the vast majority of Amazonian floodplain species have a widespread occurrence in the basin. However, our data show that abundances can vary substantially at regional scales – few species were locally abundant in more than two study areas.

Although most of the species recorded in the current study have been found elsewhere, some species appear to be registered in an Amazonian floodplain inventory for the first time. These include *Abarema longipedunculata*, *Aegiphila filipes*, *Drypetes sessiliflora*, *Heisteria perianthomega*, *Hirtella burchellii*, *Sclerobium macrophyllum* and *Tovomita acutiflora*. Due to the low abundance of many species observed in the current study and others (ter Steege et al., 2013) coupled with a paucity of floodplain forest inventories, we are unable to assess whether these species do not occur in other floodplain forests. In addition, the number of morpho-species in Amazonian inventories is often very high, making it difficult to confirm whether a species that was first registered in the present study is indeed restricted to these forests. These results clearly underline the need for additional floodplain inventories, and more work on taxonomy is required to improve species-level identifications throughout the basin. This is particularly pertinent for the conservation of nutrient-rich várzeas, as they are some of the most threatened environments in the Amazon due to logging and agricultural activities (Ohly, 2000; Junk and Piedade, 2005).

#### Acknowledgments

This research was supported by the INPA/Max Planck Project Manaus, the Brazilian Council of Science and Technology (Universal 479599/2008–4), and PRONEX CNPq-FAPEAM, Áreas Úmidas, MAUA. Assis, R.L. was supported by a doctoral scholarship from the Norwegian State Educational Loan Fund. Luize, B.G. receive grant # 2015/24554–0, São Paulo Research Foundation (FAPESP). We are grateful to Sr. José Ramos at the National Institute for Amazonian Research (INPA) Herbarium for assisting with species identifications. Special thanks to Natália Castro, Celso Rabelo Costa, José Lima, Thiago Ilnicki, Jackson de Castro, and all the field assistants who contributed to the present study. We also thank the editor and two anonymous reviewers for constructive comments on an earlier version of this manuscript.

#### Appendix A.

See Table A1.

**Table A1**

Absolute abundance of each tree species recorded in floristic inventories in floodplain forests along the Purus, Tefé, Juruá and Jutaí rivers, central-western Amazonia, Brazil.

	Juruá	Jutaí	Purus	Tefé
Anacardiaceae	5	3	11	9
<i>Spondias mombin</i> L.	5		9	
<i>Tapirira guianensis</i> Aubl		3		4
<i>Tapirira</i> sp.			2	
<i>Thyrsoodium spruceanum</i> Benth.				5
Annonaceae	200	184	96	106
<i>Anaxagorea brevipes</i> Benth.	6			
<i>Anaxagorea dolichocarpa</i> Sprague & Sandwith	2			
<i>Annona hypoglauca</i> Mart.	17		1	
<i>Annona montana</i> Macfad.		1		
<i>Bocageopsis cf. canescens</i> (Spruce ex Benth.) R.E. Fr.	20			
<i>Duguetia cf. calycina</i> Benoist				3
<i>Duguetia chrysea</i> Maas			1	
<i>Duguetia quitarensis</i> Benth.	6		8	
<i>Duguetia</i> sp.				1
<i>Duguetia spixiana</i> Mart.	4			
<i>Guatteria discolor</i> R.E. Fr.				5
<i>Guatteria inundata</i> Mart.			1	
<i>Guatteria olivacea</i> R.E. Fr.			1	25
<i>Guatteria</i> sp. 1				33
<i>Guatteria</i> sp. 2			12	
<i>Guatteria</i> sp. 3			1	
<i>Guatteria</i> sp. 4			1	
<i>Guatteria</i> sp. 5			7	
<i>Guatteria</i> sp. 6	32			
<i>Guatteria</i> sp. 7		4		
<i>Guatteria</i> sp. 8			2	
<i>Onychopetalum amazonicum</i> R.E. Fr.				2
<i>Oxandra polyantha</i> R.E. Fr.		115		
<i>Pseudoxandra polyphleba</i> (Diels) R.E.Fr. *	46	59	23	5
<i>Rollinia cuspidata</i> Mart.	2		3	
<i>Unonopsis guatterioides</i> R.E. Fr. *	40	5	30	31
<i>Xylopia amazonica</i> R.E. Fr.	19			
<i>Xylopia</i> sp. 1				1
<i>Xylopia</i> sp. 2			4	
Unidentified sp. 1			1	
Unidentified sp. 2	6			
Apocynaceae	88	68	58	19
<i>Aspidosperma nitidum</i> Benth. ex Mull.Arg.		8	3	2
<i>Aspidosperma rigidum</i> Rusby	5			
<i>Couma macrocarpa</i> Barb. Rodr.				3
<i>Himatanthus sucuuba</i> (Spruce ex Müll. Arg.) *	32	1	32	6
<i>Malouetia tamaquarina</i> (Aubl.) A. DC.	51	59		7
<i>Tabernaemontana cymosa</i> Jacq.			23	
<i>Tabernaemontana</i> sp.				1
Arecaceae	48	25	20	103
<i>Astrocaryum jauari</i> Mart. *	33	19	13	3
<i>Attalea</i> sp.			7	
<i>Euterpe precatória</i> Mart	15	6		100
Bignoniaceae	4		145	6
<i>Tabebuia barbata</i> (E. Mey.) Sandwith	1		145	6
<i>Tabebuia</i> sp.	3			
Bixaceae				8
<i>Bixa urucurana</i> Willd.				8
Boraginaceae	1	1	10	11
<i>Cordia nodosa</i> Lam. *	1	1	6	11
<i>Cordia</i> sp.1			1	
<i>Cordia</i> sp.2			1	
<i>Cordia</i> sp.3			2	
Burseraceae		25		35
<i>Crepidospermum rhoifolium</i> (Benth.) Triana & Planch.				3
<i>Protium heptaphyllum</i> (Aubl.) Marchand		25		
<i>Protium paniculatum</i> Engl.				28
<i>Protium trifoliolatum</i> Engl.				1
<i>Protium unifoliolatum</i> Engl.				3
Calophyllaceae	4	17	15	4
<i>Calophyllum brasiliense</i> Cambess. *	4	13	6	3
<i>Caraipa densifolia</i> Mart.		4		1



Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Caraipa grandifolia</i> Mart.			9	
Capparaceae	10		7	
<i>Crataeva bentharii</i> Eichler	10		7	
Caryocaraceae		12	5	8
<i>Caryocar edule</i> Casar.			2	
<i>Caryocar glabrum</i> Pers.				8
<i>Caryocar microcarpum</i> Ducke		12		
<i>Caryocar</i> sp. 1			3	
Celastraceae	1	3	11	
<i>Maytenus guianensis</i> Klotzsch		1		
<i>Salacia</i> sp. 1	1	2		
<i>Salacia</i> sp. 2			11	
Chrysobalanaceae	33	96	25	174
<i>Couepia guianensis</i> Aubl.			3	
<i>Couepia paraensis</i> (Mart. & Zucc.) Benth. ex Hook. f.		21		1
<i>Couepia</i> sp.		10		4
<i>Hirtella burchellii</i> Britton				1
<i>Hirtella</i> sp.		1		
<i>Licania bracteata</i> Prance				5
<i>Licania canescens</i> Benoist				3
<i>Licania heteromorpha</i> Benth.	2		1	
<i>Licania hirsuta</i> Prance				8
<i>Licania latifolia</i> Benth. ex Hook. f.	5			
<i>Licania longistyla</i> (Hook. f.) Fritsch		21		18
<i>Licania micrantha</i> Miq.		33		28
<i>Licania octandra</i> (Hoffmanns. ex Roem. & Schult.) Kuntze			1	12
<i>Licania pallida</i> Spruce ex Sagot			3	6
<i>Licania parvifolia</i> Huber				13
<i>Licania sclerophylla</i> (Hook. f.) Fritsch				3
<i>Licania</i> sp. 1				67
<i>Licania</i> sp. 2			1	
<i>Licania</i> sp. 3	20			
<i>Licania</i> sp. 4				5
<i>Licania</i> sp. 5	6			
<i>Licania</i> sp. 6			4	
<i>Licania</i> sp. 7			3	
<i>Licania</i> sp. 8			1	
<i>Parinari excelsa</i> Sabine		10	6	
<i>Parinari</i> sp.			2	
Clusiaceae	42	13	34	41
<i>Clusia</i> sp.				1
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi			1	
<i>Garcinia madruno</i> (Kunth) Hammel *	27	12	17	7
<i>Symphonia globulifera</i> L. f.	4			2
<i>Tovomita acutiflora</i> M. S. Barros & G. Mariz	11			
<i>Tovomita choisyana</i> Planch. & Triana				19
<i>Tovomita schomburgkii</i> Planch. & Triana		1		11
<i>Tovomita</i> sp1			12	
<i>Tovomita</i> sp2			4	
<i>Tovomita spruceana</i> Planch. & Triana				1
Combretaceae	9	15	18	19
<i>Buchenavia grandis</i> Ducke	3			
<i>Buchenavia macrophylla</i> Eichler		11		19
<i>Buchenavia oxycarpa</i> (Mart.) Eichler			14	
<i>Buchenavia</i> sp. 1			3	
<i>Buchenavia</i> sp. 2			1	
<i>Terminalia dichotoma</i> G. Mey.	6	4		
Dichapetalaceae	10	5	8	36
<i>Tapura juruana</i> (Ule) Rizzini	10	5		36
<i>Tapura</i> sp.			8	
Ebenaceae	5	38	1	13
<i>Diospyros artanthifolia</i> Mart.				4
<i>Diospyros guianensis</i> (Aubl.) Gürke		1		2
<i>Diospyros kondor</i> B. Walln.		5		
<i>Diospyros poeppigiana</i> A. DC.		32		6
<i>Diospyros</i> sp. 1				1
<i>Diospyros</i> sp. 2			1	
<i>Diospyros subrotata</i> Hiern	5			
Elaeocarpaceae	2	16	9	5

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Sloanea floribunda</i> Spruce ex Benth.		14	2	
<i>Sloanea guianensis</i> (Aubl.) Benth.	2		7	
<i>Sloanea latifolia</i> (Rich.) K. Schum.				2
<i>Sloanea nitida</i> G. Don				3
<i>Sloanea</i> sp.		2		
Emmotaceae				3
<i>Emmotum acuminatum</i> Miers				3
Erythroxylaceae	1	2	1	1
<i>Erythroxylum kapplerianum</i> Peyr.		2		1
<i>Erythroxylum</i> sp. 1	1			
<i>Erythroxylum</i> sp. 2			1	
Euphorbiaceae	187	310	155	68
<i>Alchornea castaneifolia</i> (Humb. & Bonpl. ex Willd.) A. Juss.			31	
<i>Alchornea discolor</i> Poepp.		32		2
<i>Alchornea</i> sp.			10	
<i>Alchorneopsis floribunda</i> (Benth.) Müll. Arg.	18	3		4
<i>Conceveiba guianensis</i> Aubl.	3	1		7
<i>Croton cuneatus</i> Klotzsch	39	10		1
<i>Glycydendron amazonicum</i> Ducke	2			4
<i>Glycydendron</i> sp.			3	
<i>Hevea brasiliensis</i> (Willd. ex A. Juss.) Müll. Arg.	51	63		36
<i>Hevea spruceana</i> (Benth.) Müll. Arg.	5	28	21	
<i>Hura crepitans</i> L.	7		22	
<i>Mabea caudata</i> Pax & K. Hoffm.	15			
<i>Mabea nitida</i> Spruce ex Benth.		152	1	2
<i>Mabea</i> sp.			56	
<i>Micrandra minor</i> Benth.		18		12
<i>Pera coccinea</i> (Benth.) Müll. Arg.		4		
<i>Sapium glandulosum</i> (L.) Morong			10	
<i>Sapium</i> sp. 1			1	
<i>Sapium</i> sp. 2	44			
Unidentified sp.	3			
Fabaceae	277	365	163	338
<i>Abarema longipedunculata</i> (H.S. Irwin) Barneby & J.W. Grimes		1		
<i>Abarema</i> sp. 1			3	
<i>Abarema</i> sp. 2	3			
<i>Acacia riparia</i> Kunth			11	
<i>Acosmium</i> sp.		1		
<i>Albizia</i> sp.		1		
<i>Andira inermis</i> (W. Wright) Kunth ex DC.	1			
<i>Andira</i> sp.			4	
<i>Andira trifoliolata</i> Ducke				2
<i>Batesia</i> sp.			5	
<i>Campsiandra angustifolia</i> Spruce ex Benth.	37			
<i>Campsiandra comosa</i> Benth.		21	7	8
<i>Cassia leiandra</i> Benth.			7	
<i>Chamaecrista negrensis</i> (H.S. Irwin) H.S. Irwin & Barneby				5
<i>Cassia</i> sp.			1	
<i>Clitoria amazonum</i> Mart. ex Benth.		1		
<i>Clitoria</i> sp.			1	
<i>Copaifera multijuga</i> Hayne		4		
<i>Copaifera</i> sp. 1			1	
<i>Copaifera</i> sp. 2	4			
<i>Crudia amazonica</i> Spruce ex Benth.	1	11		
<i>Cynometra bauhiniifolia</i> Benth.		1		
<i>Cynometra spruceana</i> Benth.				11
<i>Dicorynia paraensis</i> Benth.				1
<i>Dipteryx magnifica</i> Ducke				4
<i>Dipteryx odorata</i> (Aubl.) Willd.				2
<i>Etaballia dubia</i> (Kunth) Rudd	5			
<i>Heterostemon mimosoides</i> Desf.		11		
<i>Hydrochorea corymbosa</i> (Rich.) Barneby & J.W. Grimes	9	9	4	
<i>Hymenaea oblongifolia</i> Huber				1
<i>Hymenolobium pulcherrimum</i> Ducke				5
<i>Inga</i> sp. 1			3	
<i>Inga</i> sp. 2				26
<i>Inga</i> sp. 3			6	
<i>Inga</i> sp. 4			5	
<i>Inga</i> sp. 5			5	
<i>Inga</i> sp. 6			7	
<i>Inga</i> sp. 7		44		
<i>Inga</i> sp. 8			7	
<i>Inga</i> sp. 9		3		
<i>Inga</i> sp. 10				20
<i>Inga</i> sp. 11	4			

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Lecointea amazonica</i> Ducke	23			
<i>Macrolobium acaciifolium</i> (Benth.) Benth.	24	59	2	
<i>Macrolobium angustifolium</i> (Benth.) R.S. Cowan	16	44		46
<i>Macrolobium bifolium</i> (Aubl.) Pers.			8	
<i>Macrolobium multijugum</i> (DC.) Benth.				5
<i>Ormosia macrocalyx</i> Ducke	4	1	5	
<i>Ormosia paraensis</i> Ducke		1		
<i>Paramachaerium ormosioides</i> (Ducke) Ducke	1			
<i>Parkia igneiflora</i> Ducke				3
<i>Parkia multijuga</i> Benth.				2
<i>Peltogyne</i> sp.				1
<i>Platymiscium duckei</i> Huber	4			
<i>Pterocarpus amazonum</i> (Mart. ex Benth.) Amshoff			26	
<i>Pterocarpus rohrii</i> Vahl	78	100		4
<i>Pterocarpus</i> sp.				24
<i>Sclerolobium macrophyllum</i> Vogel		1		
<i>Sclerolobium</i> sp.			16	
<i>Senna silvestris</i> (Vell.) H.S. Irwin & Barneby				8
<i>Stryphnodendron polystachyum</i> (Miq.) Kleinhoonte				1
<i>Stryphnodendron</i> sp.			1	
<i>Swartzia benthamiana</i> Miq.		14		20
<i>Swartzia panacoco</i> (Aubl.) R.S. Cowan				2
<i>Swartzia</i> sp. 1				36
<i>Swartzia</i> sp. 2	1			
<i>Swartzia</i> sp. 3			8	
<i>Swartzia</i> sp. 4	1			
<i>Swartzia</i> sp. 5			2	
<i>Tachigali</i> sp.	15			
<i>Tachigali venusta</i> Dwyer		7		24
<i>Taralea oppositifolia</i> Aubl.	5	1		9
<i>Vatairea guianensis</i> Aubl. *	19	14	6	15
<i>Vouacapoua americana</i> Aubl.				1
<i>Zollernia paraensis</i> Huber		13		
<i>Zygia cataractae</i> (Kunth) L. Rico	5			22
<i>Zygia inaequalis</i> (Humb. & Bonpl. ex Willd.) Pittier	1			
<i>Zygia juruana</i> (Harms) L. Rico	16	2		28
<i>Zygia latifolia</i> (L.) Fawc. & Rendle				2
<i>Zygia</i> sp.			5	
Unidentified sp.			7	
Goupiaceae				13
<i>Goupia glabra</i> Aubl.				13
Humiriaceae			7	1
<i>Sacoglottis mattogrossensis</i> Malme			7	
<i>Sacoglottis</i> sp.				1
Hypericaceae	4	4	3	14
<i>Vismia cayennensis</i> (Jacq.) Pers.	2	1		10
<i>Vismia gracilis</i> Hieron.			3	
<i>Vismia japurensis</i> Reichardt				2
<i>Vismia macrophylla</i> Kunth	2			1
<i>Vismia sandwithii</i> Ewan		3		1
Lacistemataceae	5		9	
<i>Lacistema aggregatum</i> (P.J. Bergius) Rusby	5		8	
<i>Lacistema</i> sp.			1	
Lamiaceae	2		50	1
<i>Aegiphila filipes</i> Mart. & Schauer	2			
<i>Vitex cymosa</i> Bertero ex Spreng.			50	
<i>Vitex triflora</i> Vahl				1
Lauraceae	37	111	30	46
<i>Aniba canelilla</i> (Kunth) Mez			1	
<i>Aniba guianensis</i> Aubl.				6
<i>Aniba parviflora</i> (Meisn.) Mez				1
<i>Aniba riparia</i> (Nees) Mez	3			
<i>Aniba</i> sp. 1			1	
<i>Aniba</i> sp. 2			1	
<i>Endlicheria anomala</i> (Nees) Mez		22		
<i>Endlicheria bracteata</i> Mez				3
<i>Endlicheria ruforamula</i> Chanderbali	1			
<i>Endlicheria</i> sp.			3	
<i>Licaria guianensis</i> Aubl.				8
<i>Licaria oppositifolia</i> (Nees) Kosterm.			1	
<i>Licaria</i> sp.1			1	
<i>Licaria</i> sp.2			1	
<i>Nectandra amazonum</i> Nees	2	37		1
<i>Nectandra</i> sp.	7			

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Ocotea aciphylla</i> (Nees) Mez	9	12		10
<i>Ocotea cernua</i> (Nees) Mez	1			
<i>Ocotea costulata</i> (Nees) Mez				1
<i>Ocotea cymbarum</i> Kunth	8	10		
<i>Ocotea delicata</i> Vicent.	4			
<i>Ocotea longifolia</i> Kunth				5
<i>Ocotea myriantha</i> (Meisn.) Mez				6
<i>Ocotea</i> sp.1			2	
<i>Ocotea</i> sp.2				1
<i>Ocotea</i> sp.3		19		
<i>Ocotea</i> sp.4			4	
<i>Ocotea</i> sp.5		11		
<i>Ocotea</i> sp.6			10	
<i>Ocotea</i> sp.7			2	
<i>Ocotea</i> sp.8	2			
<i>Rhodostemonodaphne kunthiana</i> (Nees) Rohwer				4
<i>Rhodostemonodaphne</i> sp.			1	
Unidentified sp. 1			1	
Unidentified sp. 2			1	
<b>Lecythidaceae</b>	<b>105</b>	<b>239</b>	<b>63</b>	<b>216</b>
<i>Couratari tenuicarpa</i> A.C. Sm.				8
<i>Couratari</i> sp.				2
<i>Couroupita subsessilis</i> Pilg.	10		9	
<i>Eschweilera albiflora</i> (DC.) Miers *	1	106	26	136
<i>Eschweilera coriacea</i> (DC.) S.A. Mori	31			
<i>Eschweilera ovalifolia</i> (DC.) Nied.	45	91	5	
<i>Eschweilera parviflora</i> (Aubl.) Miers				13
<i>Eschweilera</i> sp1				5
<i>Eschweilera</i> sp2			15	
<i>Gustavia augusta</i> L. *	16	39	4	3
<i>Gustavia hexapetala</i> (Aubl.) Sm.			4	
<i>Lecythis poiteaui</i> O. Berg		1		4
<i>Lecythis prancei</i> S.A. Mori	2	2		45
<b>Malpighiaceae</b>	<b>16</b>	<b>3</b>	<b>4</b>	<b>1</b>
<i>Byrsonima incarnata</i> Sandwith	4			1
<i>Byrsonima japurensis</i> A. Juss.	12		4	
<i>Byrsonima</i> sp.		3		
<b>Malvaceae</b>	<b>144</b>	<b>29</b>	<b>276</b>	<b>31</b>
<i>Apeiba glabra</i> Aubl.			2	
<i>Apeiba</i> sp.				4
<i>Bombacopsis paraensis</i> (Ducke) A. Robyns				2
<i>Chorisia</i> sp.	1	6		
<i>Luehea cymulosa</i> Spruce ex Benth.		6	108	
<i>Lueheopsis rosea</i> (Ducke) Burret	34			5
<i>Matisia ochrocalyx</i> K. Schum.	4			
<i>Mollia</i> sp.		12		
<i>Pachira aquatica</i> Aubl.		1		
<i>Pachira insignis</i> (Sw.) Sw. ex Savigny	8		9	
<i>Pseudobombax munguba</i> (Mart. & Zucc.) Dugand *	15	1	148	6
<i>Quararibea guianensis</i> Aubl.	78			
<i>Quararibea ochrocalyx</i> (K. Schum.) Vischer			5	
<i>Quararibea</i> sp. 1				2
<i>Quararibea</i> sp. 2		1		
<i>Sterculia</i> sp.		2		
<i>Theobroma cacao</i> L.	4		4	
<i>Theobroma obovatum</i> Klotzsch ex Bernoulli				7
<i>Theobroma subincanum</i> Mart.				5
<b>Melastomataceae</b>		<b>2</b>	<b>7</b>	<b>9</b>
<i>Miconia</i> sp. 1			3	
<i>Miconia</i> sp. 2			1	
<i>Miconia</i> sp. 3				1
<i>Mouriri grandiflora</i> DC.				4
<i>Mouriri</i> sp. 1				4
<i>Mouriri</i> sp. 2			1	
<i>Mouriri</i> sp. 3			2	
<i>Mouriri</i> sp. 4		2		
<b>Meliaceae</b>	<b>16</b>	<b>16</b>	<b>25</b>	<b>6</b>
<i>Carapa guianensis</i> Aubl.		4		
<i>Guarea guidonia</i> (L.) Sleumer	10		13	6
<i>Guarea purusana</i> C. DC.		1		
<i>Trichilia rubra</i> C. DC.	6			
<i>Trichilia</i> sp. 1			12	

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Trichilia</i> sp. 2		11		
Moraceae	30	131	60	74
<i>Batocarpus amazonicus</i> (Ducke) Fosberg			6	
<i>Batocarpus</i> sp.	3			
<i>Brosimum lactescens</i> (S. Moore) C.C. Berg *	5	109	22	9
<i>Brosimum rubescens</i> Taub.				24
<i>Brosimum</i> sp. 1				20
<i>Brosimum</i> sp. 2			1	
<i>Brosimum</i> sp. 3			6	
<i>Clarisia biflora</i> Ruiz & Pav.	1			
<i>Ficus</i> sp. 1			1	
<i>Ficus</i> sp. 2			1	
<i>Ficus</i> sp. 3			1	
<i>Ficus</i> sp. 4	11			
<i>Helicostylis</i> sp. 1				1
<i>Helicostylis</i> sp. 2			1	
<i>Helicostylis</i> sp. 3		7		
<i>Helicostylis</i> sp. 4			1	
<i>Maquira coriacea</i> (H. Karst.) C.C. Berg			17	
<i>Maquira guianensis</i> Aubl.				1
<i>Naucleopsis uli</i> (Warb.) Ducke				8
<i>Pseudolmedia laevis</i> (Ruiz & Pav.) J.F. Macbr.	8	8		8
<i>Sorocea guilleminiana</i> Gaudich.		7		
<i>Sorocea hirtella</i> Mildbr.	2			
<i>Sorocea</i> sp.			3	
<i>Trymatococcus amazonicus</i> Poepp. & Endl.				3
Myristicaceae	146	70	67	70
<i>Iryanthera juruensis</i> Warb.	3	9	3	
<i>Iryanthera</i> sp. 1				2
<i>Iryanthera</i> sp. 2			5	
<i>Viola calophylla</i> (Spruce) Warb. *	7	22	10	11
<i>Viola elongata</i> (Benth.) Warb.			2	
<i>Viola surinamensis</i> (Rol. ex Rottb.) Warb. *	136	39	47	34
<i>Viola theiodora</i> (Spruce ex Benth.) Warb.				23
Myrtaceae	20	24	56	65
<i>Calyptranthes crebra</i> McVaugh		1		9
<i>Calyptranthes</i> sp. 1			2	
<i>Calyptranthes</i> sp. 2			1	
<i>Calyptranthes</i> sp. 3			1	
<i>Eugenia acrensis</i> McVaugh	5			
<i>Eugenia cupulata</i> Amshoff		17		
<i>Eugenia egensis</i> DC.	2			
<i>Eugenia gomesiana</i> O. Berg				8
<i>Eugenia patrisii</i> Vahl		3		
<i>Eugenia</i> sp. 1			9	
<i>Eugenia</i> sp. 2				4
<i>Eugenia</i> sp. 3				1
<i>Eugenia</i> sp. 4			13	
<i>Eugenia</i> sp. 5			6	
<i>Eugenia</i> sp. 6			3	
<i>Eugenia</i> sp. 7			2	
<i>Eugenia</i> sp. 8				5
<i>Eugenia</i> sp. 9			2	
<i>Eugenia</i> sp. 10			1	
<i>Myrcia aliena</i> McVaugh				3
<i>Myrcia amazonica</i> DC.				31
<i>Myrcia fallax</i> (Rich.) DC.				2
<i>Myrcia magnoliifolia</i> DC.	6			
<i>Myrcia</i> sp. 1			3	
<i>Myrcia</i> sp. 2			2	
<i>Myrcia</i> sp. 3		2		
<i>Myrciaria dubia</i> (Kunth) McVaugh	1	1		
<i>Psidium</i> sp. 1			1	
<i>Psidium</i> sp. 2			2	
<i>Psidium</i> sp. 3			7	
Unidentified sp.1				2
Unidentified sp.2	4			
Unidentified sp.3	2			
Unidentified sp.4			1	
Nyctaginaceae	31	13	2	8
<i>Neea oppositifolia</i> Ruiz & Pav.				8
<i>Neea</i> sp. 1		13		
<i>Neea</i> sp. 2			1	
<i>Neea</i> sp. 3	31			
<i>Neea</i> sp. 4			1	

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
Ochnaceae				3
<i>Lacunaria crenata</i> (Tul.) A.C. Sm.				1
<i>Ouratea discophora</i> Ducke				2
Olacaceae	5	30	8	14
<i>Heisteria acuminata</i> (Humb. & Bonpl.) Engl.	3		5	12
<i>Heisteria perianthomega</i> (Vell.) Sleumer	2			
<i>Heisteria spruceana</i> Engl.		28		
<i>Minquartia guianensis</i> Aubl.		2	3	2
Phyllanthaceae		43		2
<i>Amanoa guianensis</i> Aubl.				2
<i>Amanoa oblongifolia</i> Müll. Arg.		33		
<i>Discocarpus spruceanus</i> Müll. Arg.		10		
Picramniaceae			1	
<i>Picramnia latifolia</i> Tul.			1	
Picrodendraceae			53	
<i>Piranhea trifoliata</i> Baill.			53	
Polygonaceae	12	8	79	4
<i>Coccoloba charitostachya</i> Standl.				1
<i>Coccoloba latifolia</i> Lam.		1		
<i>Coccoloba ovata</i> Benth.		5		
<i>Coccoloba</i> sp. 1			1	
<i>Coccoloba</i> sp. 2			34	
<i>Coccoloba</i> sp. 3			2	
<i>Coccoloba</i> sp. 4	3			
<i>Symmeria paniculata</i> Benth.		1	9	
<i>Triplaris</i> sp.				3
<i>Triplaris weigeltiana</i> (Rchb.) Kuntze	9	1	33	
Proteaceae		6	3	2
<i>Panopsis rubescens</i> (Pohl) Rusby		6		2
<i>Panopsis sessilifolia</i> (Rich.) Rich.			2	
Unidentified sp.			1	
Putranjivaceae	7		6	
<i>Drypetes amazonica</i> Steyerm.	7			
<i>Drypetes sessiliflora</i> Allemão			2	
<i>Drypetes</i> sp. 1			3	
<i>Drypetes</i> sp. 2			1	
Rubiaceae	31	49	19	12
<i>Amaioua corymbosa</i> Kunth	8			
<i>Amaioua</i> sp.			1	
<i>Bothriospora corymbosa</i> (Benth.) Hook. f.	2			
<i>Calycophyllum spruceanum</i> (Benth.) Hook. f. ex K. Schum.		26		
<i>Chimarrhis barbata</i> (Ducke) Bremek.	3	7		
<i>Coussarea hirticalyx</i> Standl.			2	
<i>Duroia genipoides</i> Hook. f. ex K. Schum.		7	3	7
<i>Duroia macrophylla</i> Huber		2		
<i>Faramea occidentalis</i> (L.) A. Rich.		6		3
<i>Faramea</i> sp.			1	
<i>Ferdinandusa</i> sp.			2	
<i>Genipa americana</i> L.	5			
<i>Pagamea</i> sp. 1			6	
<i>Pagamea</i> sp. 2			4	
<i>Palicourea crocea</i> (Sw.) Roem. & Schult.				1
<i>Randia armata</i> (Sw.) DC.	1			
<i>Sickingia tinctoria</i> (Aubl.) Lemée	12	3		
Unidentified sp.				1
Rutaceae	1		3	
<i>Zanthoxylum compactum</i> (Huber ex Albuquerque) P.G. Waterman	1		2	
<i>Zanthoxylum</i> sp.			1	
Salicaceae	1	3	38	3
<i>Banara arguta</i> Briq.			27	
<i>Casearia manausensis</i> Sleumer		1		
<i>Casearia pitumba</i> Sleumer				3
<i>Casearia</i> sp. 1	1			
<i>Casearia</i> sp. 2			1	
<i>Homalium</i> sp.		2		
<i>Laetia corymbulosa</i> Spruce ex Benth.			10	
Sapindaceae	1	16	8	2
<i>Allophylus amazonicus</i> (Mart.) Radlk.	1			
<i>Cupania scrobiculata</i> Rich.		8	1	
<i>Cupania</i> sp. 1				1
<i>Cupania</i> sp. 2		2		

Table A1 (Continued)

	Juruá	Jutaí	Purus	Tefé
<i>Matayba macrostylis</i> Radlk.			2	
<i>Matayba</i> sp.			5	
<i>Toulicia guianensis</i> Aubl.		6		
Unidentified sp.				1
<b>Sapotaceae</b>	89	145	153	94
<i>Chrysophyllum argenteum</i> Jacq.	12		1	
<i>Chrysophyllum sanguinolentum</i> (Pierre) Baehni		2		19
<i>Ecclinusa lanceolata</i> (Mart. & Eichler) Pierre		11		2
<i>Ecclinusa</i> sp.				5
<i>Manilkara bidentata</i> (A. DC.) A. Chev.			4	
<i>Manilkara</i> sp.				3
<i>Micropholis casiquiarensis</i> Aubrév.				2
<i>Micropholis egensis</i> (A. DC.) Pierre	4		7	
<i>Micropholis guyanensis</i> (A. DC.) Pierre		3		
<i>Micropholis</i> sp.			1	
<i>Micropholis venulosa</i> (Mart. & Eichler) Pierre		16		8
<i>Pouteria anomala</i> (Pires) T.D. Penn.		2		
<i>Pouteria caimito</i> (Ruiz & Pav.) Radlk.	5			
<i>Pouteria campanulata</i> Baehni	16			
<i>Pouteria elegans</i> (A. DC.) Baehni		27	87	15
<i>Pouteria eugenifolia</i> (Pierre) Baehni	2			
<i>Pouteria glomerata</i> (Miq.) Radlk.	14		1	4
<i>Pouteria gomphiiifolia</i> (Mart. ex Miq.) Radlk.		8		
<i>Pouteria laevigata</i> (Mart.) Radlk.			14	1
<i>Pouteria macrophylla</i> (Lam.) Eyma			9	10
<i>Pouteria procera</i> (Mart.) K. Hammer	8		12	
<i>Pouteria torta</i> (Mart.) Radlk.				3
<i>Pouteria venosa</i> (Mart.) Baehni				1
<i>Pouteria</i> sp. 1			8	
<i>Pouteria</i> sp. 2				3
<i>Pouteria</i> sp. 3		8		
<i>Pouteria</i> sp. 4				7
<i>Pouteria</i> sp. 5	4			
<i>Pouteria</i> sp. 6		41		
<i>Pouteria</i> sp. 7				11
<i>Pouteria</i> sp. 8	24			
<i>Pouteria</i> sp. 9		12		
<i>Pouteria</i> sp. 10		14		
<i>Pouteria</i> sp. 11			7	
<i>Pradosia</i> sp. 1			2	
<i>Pradosia</i> sp. 2		1		
<b>Simaroubaceae</b>	10	13	31	9
<i>Simaba guianensis</i> Aubl.			31	
<i>Simaba orinocensis</i> Kunth	10	13		9
<b>Siparunaceae</b>		10		
<i>Siparuna cristata</i> (Poepp. & Endl.) A. DC.		10		
<b>Urticaceae</b>	50	8	4	17
<i>Cecropia distachya</i> Huber			1	
<i>Cecropia latiloba</i> Miq.		5	1	
<i>Cecropia</i> sp. 1				3
<i>Cecropia</i> sp. 2	44			
<i>Coussapoa</i> sp. 1		3		
<i>Coussapoa</i> sp. 2	5			
<i>Pourouma</i> sp. 1				14
<i>Pourouma</i> sp. 2	1			
<i>Pourouma</i> sp. 3			2	
<b>Violaceae</b>	155	61	20	26
<i>Amphirrhox longifolia</i> (A. St.-Hil.) Spreng.		4	5	
<i>Leonia crassa</i> L.B. Sm. & A. Fernández	148			1
<i>Leonia glycyarpa</i> Ruiz & Pav.		53	15	5
<i>Paypayrola grandiflora</i> Tul.				20
<i>Rinorea</i> sp.		4		
<i>Rinoreocarpus ulei</i> (Melch.) Ducke	7			
<b>Vochysiaceae</b>		10		
<i>Erismia calcaratum</i> (Link) Warm.		10		
<b>Unidentified</b>				
Â Unidentified sp. 1			2	
Â Unidentified sp. 2			1	
Â Unidentified sp. 3			1	
Â Unidentified sp. 4	1			

Species name followed by a star (\*) occurred across all four study areas.

## Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.flora.2017.02.019>.

## References

- Albernaz, A.L., Pressey, R.L., Costa, L.R.F., Ramos, F., Assunção, P.A., Moreira, M.P., Franciscan, C.H., 2012. Tree species compositional change and conservation implications in the white-water flooded forests of the Brazilian Amazon. *J. Biogeogr.* 39, 869–883.
- Assis, R.L., Wittmann, F., 2011. Forest structure and tree species composition of the understory of two Central Amazonian várzea forests of contrasting flood heights. *Flora* 206, 251–260.
- Assis, R.L., Wittmann, F., Piedade, M.T.F., Haugaasen, T., 2015a. Effects of hydroperiod and substrate properties on tree alpha diversity and composition in Amazonian floodplain forests. *Plant Ecol.* 216, 41–54.
- Assis, R.L., Haugaasen, T., Schöngart, J., Montero, J.C., Piedade, M.T.F., Wittmann, F., 2015b. Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. *J. Veg. Sci.* 26, 312–322.
- Ayres, J.M., 1993. *As Matas De várzea Do Mamirauá MCT/CNPq – Sociedade. Civil Mamirauá, Brasília.*
- Balslev, H., Lutteyn, J., Yllgaard, B., Holm-Nielsen, L., 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92, 37–57.
- Campbell, D.G., Daly, D.C., Prance, G.T., Maciel, U.N., 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* 38, 369–393.
- Campbell, D.G., Stone, J.L., Rosas, A., 1992. A comparison of the phytosociology and dynamics of three floodplain (Várzea) forests of known ages Rio Juruá, western Brazilian Amazon. *Zool. J. Linn. Soc.* 108, 213–237.
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Condit, R.S.P., Hubbell, S.P., Foster, R.B., 1996. Changes in tree species abundance in a neotropical forest: impact of climate change. *J. Trop. Ecol.* 12, 231–256.
- Coronado, E.N.H., Baker, T.R., Phillips, O.L., Pitman, N.C.A., Pennington, R.T., Vasquez-Martinez, R., Monteagudo, A., Mogollon, H., Davila-Cardozo, N., Rios, M., et al., 2009. Multi-scale comparisons of tree composition in Amazonian terra firme forests. *Biogeosciences* 6, 2719–2731.
- Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie forest border region of Wisconsin. *Ecology* 32, 476–496.
- Dexter, K.G., Terborgh, J.W., Cunningham, C.W., 2012. Historical effects on beta diversity and community assembly in Amazonian trees. *Proc. Natl. Acad. Sci. U. S. A.* 109, 7787–7792.
- Ducke, A., 1913. Explorações científicas no Estado do Pará. *Bol. Mus. Para. Emílio Goeldi* 7, 100–198.
- Duque, A., Sanchez, M., Cavelier, J., Duivenvoorden, J.F., 2002. Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *J. Trop. Ecol.* 18, 499–525.
- Fernandes-Corrêa, A.F., Furch, B., 1992. Investigations on the tolerance of several trees to submergence in blackwater (Igapó) and whitewater (Várzea) inundation forests near Manaus, Central Amazonia. *Amazoniana* 12, 71–84.
- Ferreira, L.V., Prance, G.T., 1998. Structure and species richness of low-diversity floodplain forest on the Rio Tapajós, Eastern Amazonia. *Brazil Biodivers. Conserv.* 7, 585–596.
- Ferreira, L.V., Stohlgren, T.J., 1999. Effects of river level fluctuation on plant species richness, diversity and distribution in a floodplain forest in Central Amazonia. *Oecologia* 120, 582–587.
- Ferreira, L.V., 1997. Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jaú National Park in floodplain forests in central Amazonia. *Biodivers. Conserv.* 6, 1353–1363.
- Ferreira, L.V., 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. *Biodivers. Conserv.* 9, 1–14.
- Fisher, A.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42–58.
- Gentry, A.H., Ortiz, S.R., 1993. *Padrones de composición florística em la Amazonia Peruana.* In: Kalliola, R., Puhakka, M., Danjoy, W. (Eds.), *Amazonia Peruana. PAUT and ONERN, Jyväskylä (Finland)*, pp. 155–166.
- Gentry, A.H., 1988. Tree species richness of upper Amazonian forests. *Proc. Natl. Acad. Sci. U. S. A.* 85, 156–159.
- Gentry, A.H., 1992. Tropical forest biodiversity distributional patterns and their conservation significance. *Oikos* 63, 19–28.
- Goulding, M., 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. In: Kubitzki, K. (Ed.), *Dispersal and Distribution. Sonderarbeiten d. Naturwiss, Hamburg*, pp. 271–283.
- Haugaasen, T., Peres, C., 2006. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia. *Brazil. Acta Amaz.* 36, 25–36.
- Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soulé, M. (Ed.), *Conservation Biology: Science of Scarcity and Diversity.* Sinauer Associates, Sunderland, MA (USA), pp. 205–231.
- Huber, J., 1906. La vegetation de la vale de Rio Purus. *Bull. Herb. Boissier* 4, 249–289.
- Huber, J., 1910. Matas e madeiras amazônicas. *Bol. Mus. Para. Emílio Goeldi* 6, 91–225.
- Junk, W.J., Piedade, M.T.F., 2005. Amazonian wetlands. In: Fraser, L.H., Keddy, P.A. (Eds.), *Large Wetlands: Their Ecology and Conservation.* Cambridge University Press, Cambridge (UK), pp. 63–117.
- Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-haft, M., Adeney, J.M., Wittmann, F., 2011. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31, 623–640.
- Junk, W.J., 1989. Flood tolerance and tree distribution in central Amazonian floodplains. In: Holm-Nielsen, L.B., Nielsen, I.C., Balslev, H. (Eds.), *Tropical Forests: Botanical Dynamics, Speciation and Diversity.* Academic Press, London, pp. 47–64.
- Kalliola, R., Salo, J., Puhakka, M., Rajasilta, M., 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. *J. Ecol.* 79, 877–901.
- Keel, S.H., Prance, G.T., 1979. Studies of the vegetation of a black water igapó (rio Negro – Brazil). *Acta Amaz.* 9, 645–655.
- Kubitzki, K., Ziburski, A., 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26, 30–43.
- Kubitzki, K., 1989. The ecogeographical differentiation of Amazonian inundation forests. *Plant Syst. Evol.* 163, 285–304.
- Lopez, O.R., 2001. Seed flotation and post flooding germination in tropical terra firme and seasonally flooded forest species. *Funct. Ecol.* 15, 763–771.
- Melack, J.M., Hess, L.L., 2010. Remote sensing of the distribution and extent of wetlands in the Amazon basin. In: Junk, W.J., Piedade, M.T.F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management.* Springer Verlag, Berlin, pp. 44–59.
- Minchin, P.R., 1987. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* 71, 145–156.
- Montero, J.C., Piedade, M.T.F., Wittmann, F., 2012. Floristic variation across 600 km of inundation forests (igapó) along the Negro River, Central Amazonia. *Hydrobiologia* 729, 229–246.
- Mori, S.A., Boom, B.M., De Carvalho, A.M., Santos, T.S., 1983. Ecological importance of Myrtaceae in an eastern Brazilian wet forest. *Biotropica* 15, 68–70.
- Mori, S.A., Becker, P., Kincaid, D., 2001. Lecythidaceae of a central Amazonian lowland forest: implications for conservation. In: Bierregaard, R.O.J., Gascon, C., Lovejoy, T.E., Mesquita, R.C.G. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented.* Yale University Press, New Haven (USA) & London, pp. 54–67.
- Ohly, J.J., 2000. Development of Central Amazon in the modern era. In: Junk, W.J., Ohly, J.J., Piedade, M.T.F., Soares, M.G.M. (Eds.), *The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management.* Backhuys Publishers Bv, Leiden (Netherlands), pp. 27–73.
- Oksanen, J., 2005. *Multivariate Analysis of Ecological Communities in R: Vegan Tutorial.* University of Oulu, Finland.
- Parolin, P., Ferreira, L.V., Albernaz, A.L., Almeida, S.S., 2004. Tree species distribution in várzea forests of Brazilian Amazonia. *Folia Geobot.* 39, 371–383.
- Parolin, P., 2000. Phenology and CO<sub>2</sub> assimilation of trees in Central Amazonian floodplains. *J. Trop. Ecol.* 16, 465–473.
- Parolin, P., 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* 128, 326–335.
- Pitman, N.C.A., Terborgh, J., Silman, M.R., Nuñez-Vargas, P., 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80, 2651–2661.
- Pitman, N.C.A., Terborgh, J., Silman, M.R., Nuñez-Vargas, P., Neill, D.A., Ceron, C.E., Palacios, W.A., Aulestia, M., 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82, 2102–2117.
- Prance, G.T., 1979. Notes on the vegetation of Amazonia 3: the terminology of Amazonian forest types subject to inundation. *Brittonia* 31, 26–38.
- Schlüter, U.B., Furch, B., Joly, C.A., 1993. Physiological and anatomical adaptations by young *Astrocaryum jauari* Mart. (Arecaceae) in periodically inundated biotopes of central Amazonia. *Biotropica* 25, 384–396.
- Schongart, J., Piedade, M.T.F., Wittmann, F., Junk, W.J., Worbes, M., 2005. Wood growth patterns of *Macrobolium acciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black water and white-water floodplain forests. *Oecologia* 145, 454–461.
- Schulman, L., Toivonen, T., Ruokolainen, K., 2007. Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *J. Biogeogr.* 34, 1388–1399.
- Sombroek, W., 2001. Spatial and temporal patterns of Amazon rainfall – Consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* 30, 388–396.
- Spruce, R., 1908. *Notes of a Botanist in the Amazon and Andes.* MacMillan, London.
- Terborgh, J., Andresen, E., 1998. The composition of Amazonian forests: patterns at local and regional scales. *J. Trop. Ecol.* 14, 645–664.
- Terborgh, J., Pitman, N., Silman, M., Schichter, H., Nunez, P.V., 2002. Maintenance of tree diversity in tropical forests. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation.* CAB International, Wallingford (UK), pp. 1–17.
- Tuomisto, H., Ruokolainen, K., 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *J. Veg. Sci.* 5, 25–34.



- Wittmann, F., Junk, W.J., 2003. Sapling communities in Amazonian white-water forests. *J. Biogeog.* 30, 1533–1544.
- Wittmann, F., Anhof, D., Junk, W.J., 2002. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.* 18, 805–820.
- Wittmann, F., Junk, W.J., Piedade, M.T.F., 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *Forest Ecol. Manag.* 196, 199–212.
- Wittmann, F., Schöngart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., Queiroz, H.L.D., Worbes, M., 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *J. Biogeogr.* 33, 1334–1347.
- Wittmann, F., Schöngart, J., Junk, W.J., 2010. Phytogeography, species diversity, community structure and dynamics of Amazonian floodplain forests. In: Junk, W.J., Piedade, M.T.F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer Verlag, Berlin, pp. 61–104.
- Wittmann, F., Householder, E., Piedade, M.T.F., Assis, R.L., Schöngart, J., Parolin, P., Junk, W.J., 2013. Habitat specificity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. *Ecography* 35, 1–18.
- Worbes, M., Klinge, H., Revilla, J.D., Martius, C., 1992. On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. *J. Veg. Sci.* 3, 553–564.
- Worbes, M., 1997. The forest ecosystem of the floodplains. In: Junk, W.J. (Ed.), *The Central Amazon Floodplain: Ecology of a Pulsing System*. Ecological Studies 126. Springer, Berlin, pp. 223–265.
- ter Steege, H., Sabatier, S., Castellanos, H., van Andel, T., Duivenvoorden, J., de Oliveira, A.A., Ek, R.C., Lilwah, R., Maas, P.J.M., Mori, S.A., 2000. An analysis of Amazonian floristic composition, including those of the Guiana Shield. *J. Trop. Ecol.* 16, 801–828.
- ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., et al., 2003. A spatial model of tree  $\alpha$ -diversity and tree density for the Amazon. *Biod. Cons.* 12, 2255–2277.
- ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F., Prévost, M.F., Spichiger, R., Castellanos, H., et al., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443, 444–447.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C.V., Magnusson, W.E., Molino, J.F., et al., 2013. Hyperdominance in Amazonian tree flora. *Science* 342, 325–334.