Structure and Composition of Terra Firme and Seasonally Flooded Várzea Forests in the Western Brazilian Amazon

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Abstract: *Research Highlights*: Rare, or sparsely distributed, species drive the floristic diversity of upland, terra firme and seasonally flooded forests in the central Juruá—a remote and hitherto floristically poorly known area in the Brazilian Amazon. *Background and Objectives*: Floristic inventories are critical for modelling and understanding the role of Amazonian forests in climate regulation, for sustainable management of forest resources and efficient conservation planning. Yet, detailed information about the often complex spatial distributions of many Amazonian woody plants is limited. Here, we provide information about forest structure and species composition from a remote terra firme forest and an adjacent floodplain forest in the western Brazilian Amazon. More specifically, we ask (1) how floristically different are the terra firme and floodplain forests? and (2) how variable is species composition within the same forest type? *Materials and Methods*: Between September 2016 and October 2017, we inventoried 97 plots (each 0.1 ha; 100 × 10 m) placed at least 800 m apart, with 46 plots in terra firme forest and 51 in seasonally flooded forest. We included all trees, hemi-epiphytes and palms with diameter at breast height (dbh) > 10 cm and woody lianas > 5 cm dbh. We examine forest structure, family- and species-level floristic composition and species diversity within and between forest types using family and species importance values, rarefaction curves and dissimilarity matrices. *Results*: Terra firme forest and seasonally flooded forest woody plant communities differ both in structure and species composition, which was highly variable within forest types. Many species were shared between terra firme and seasonally flooded forests, but most species were forest type-specific. Whereas species richness was greatest in the terra firme forest, floodplain species richness was among the highest regionally. *Conclusions*: Floodplain forests are a crucial complement to terra firme forests in terms of Amazonian woody plant diversity.

Keywords: Amazon; forest structure; floodplain forest; paleo-várzea; plant diversity; species composition; terra firme; várzea; woody plants

1. Introduction

Floristic inventories are critical for modelling and understanding the role of Amazonian forests in climate regulation, for sustainable management of forest resources and efficient conservation planning. Yet, for a number of reasons, floristic inventories in Amazonian forests are notoriously difficult and detailed information about the often complex spatial distributions of many Amazonian trees is

limited [1–4]. Additionally, the majority of published floristic inventories have been conducted close to urban centres [5] and focus on terra firme forests [6]. This results in severe biases in our knowledge of tree species richness and distribution, and many remote areas remain neglected and poorly represented in herbaria [7,8].

Considering the irregular distribution and local rarity of many tropical tree species [9], the bias and patchiness of floristic data from the Amazon presents one of the biggest challenges for conservation biologists and climate modellers alike. Although it is the largest remaining tract of tropical forest on Earth, the status of the Amazon is precarious, as threats from deforestation, logging and other disturbances continue to increase [10–13]. Such activities adversely affect forest structure and composition, as well as the forest capacity to store carbon, retain water and regulate climate [14–19]. Thus, we urgently need on-the-ground efforts to improve our forest inventory coverage.

Broadly speaking, Amazonian forests may be divided into upland forests (hereafter, terra firme) that lie above the maximum flood level of rivers and perennial streams, and lowland, forested wetlands that are either seasonally or permanently inundated. In general, closed-canopy terra firme forests lie on well-drained terrains that tend to be heavily leached and nutrient-poor [20,21]. However, some terra firme forests, such as the forests on the elevated terraces alongside the floodplains of the Juruá River, have relatively nutrient-rich soils as they occupy substrates that were once eutrophic floodplains. Such lowland terra firme forests typically fringe the seasonally inundated floodplains but are no longer under the influence of the monomodal flood pulse that dominate the floodplains.

Seasonally flooded forests comprise the second major forest type in the Amazon [22]. Because of the lowland topography of the basin and the high seasonality in rainfall, forests in central Amazonia may endure floods lasting up to 210 days per year and reaching 10–15 m in amplitude [23]. Depending on the hydro-chemical and floristic characteristics, these floodplain forests are divided into seven main types [24]. Of these, the most extensive floodplain forests are those inundated by white-water rivers (e.g., the Amazonas/Solimões, Madeira, Purús and Juruá), and are called várzea. Because the rivers that flood várzea forests drain Andean landscapes that are geologically young and easily erode [25], they bring large amounts of suspended nutrient-rich sediments onto the floodplains [26–28]. These sediments give the rivers their muddy appearance and leave the várzea floodplains eutrophic, species-rich and exceptionally productive [29].

Floodplain forests are severely under-represented in herbaria, with a collection density for wetland forests averaging only 0.05 records per 100 km^2 [6] and many botanical samples lack information about detailed habitat conditions. Várzeas are the best-collected category of floodplain forests in Amazonia, but although a highly important floristic region, inventories have been particularly scarce in the Juruá River region [5]. Moreover, while terra firme forests are comparatively well-represented in Amazonian forest inventories, few studies recognise and focus on the lowland terra firme forests that grow on old eutrophic floodplain sediments (paleo-várzea sediments) adjacent to seasonally inundated várzeas [30]. The Juruá floodplain, with its extensive stretch of adjacent flooded and terra firme forests, is therefore a priority area for botanical inventories to improve our knowledge on Amazonian tree diversity [6].

Here, we present a floristic inventory from lowland terra firme forest and adjacent seasonally inundated várzea forest from the central Juruá River basin. More specifically, we ask (1) how floristically different are terra firme and várzea forests? and (2) how variable is species composition among plots within the same forest type? We use species rarefactions and dissimilarity indices to examine these differences in structure and composition within and between terra firme and várzea forests. We discuss our findings in relation to wider patterns of forest structure and species distributions in the Amazon basin and conclude that várzea forests are an important complement to terra firme forests.

2. Materials and Methods

2.1. Study Area

This study took place in the central Juruá River basin, western Brazilian Amazonia. The region contains both seasonally flooded várzea (VZ) and lowland terra firme forests on paleo-várzea sediments (TF). The study area was located between 05°08′ S, 67°01′ W and 05°87′ S, 67°88′ W and includes the Uacari Sustainable Development Reserve (RDS Uacari, 632,949 ha), but excludes the Médio Juruá Extractive Reserve (ResEx Médio Juruá, 253,227 ha; Figure 1). The climate of the region is wet and tropical. Annual temperatures and rainfall average 27.1 °C and 3679 mm, respectively [31]. The elevation within the inventoried forests ranges from 67 to 153 m above sea level for terra firme and 68–137 m above sea level for várzea. The forests represent structurally intact vegetation.
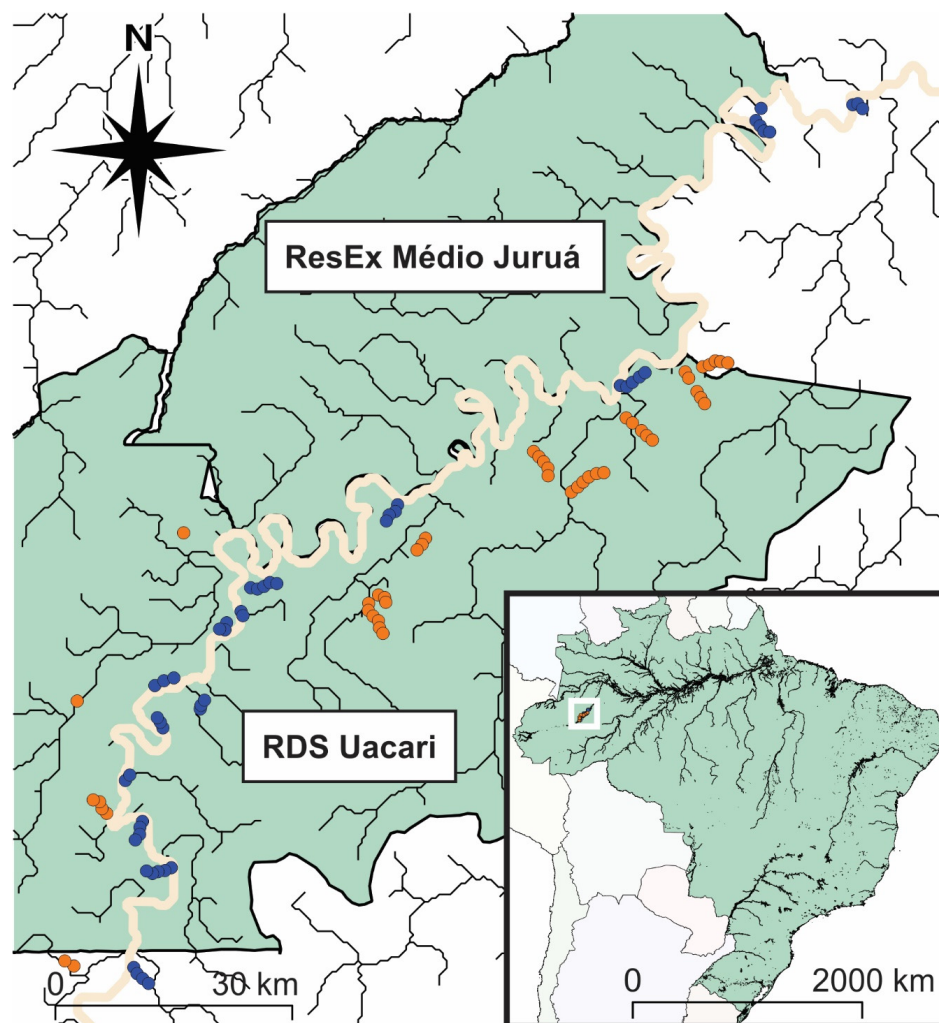

Figure 1. Map showing the study area in western Brazilian Amazonia (indicated by the white square in the inset map) and plot locations of woody plant inventories in terra firme (orange) and várzea forests (dark blue) along 150 km of the Juruá River (in beige). Smaller rivers are shown as black lines. The Médio Juruá Extractive Reserve (ResEx Médio Juruá) and Uacari Sustainable Development Reserve (RDS Uacari) are shown in green with black borders. The map was generated in QGIS v.3.12.2, using background maps from the GADM database of Global Administrative Areas [32]. The shapefiles for the ResEx Médio Juruá and RDS Uacari were provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and the Amazonas State Environmental Agency (SEMA-DEMUC), respectively.

2.2. Floristic Inventories and Measurements

Between September 2016 and October 2017, we inventoried 97 plots (each 0.1 ha; 100 × 10 m), with 46 plots in terra firme forest (TF) and 51 in seasonally flooded várzea forest (VZ). The shortest distance between inventory plots was 800 m. To capture várzea forest at different inundation depths and periodicity as well as different soil types, topographic conditions and microhabitats, the plots were placed along transects that extended along the flooding gradient, with increasing elevation at greater distances from the main river channel.

Within each plot, all trees, hemi-epiphytes and palms ≥ 10 cm diameter at breast height (dbh), and all woody lianas ≥ 5 cm dbh, were measured and identified. Peripheral individuals straddling the boundary of the plots were included in the inventory if the mid-point of their trunks fell within the plot. We measured the dbh of buttressed trees immediately above the buttresses. When direct measurement with a dbh-tape was not possible (e.g., sulcate trunks, stranglers or where buttresses were too high), we estimated the diameters. We used a Haglöf Vertex IV and Transponder T3 to measure tree, palm and hemi-epiphyte total heights based on trigonometric calculations using the measuring angle and distance to the trunk [33], and/or estimated total heights where this was not possible. For trees and hemi-epiphytes, we also determined the height of the first branch. For palms, we determined the height of the stem. To remove observer bias, the same person (Y.K.B.) administered all height measurements.

All individuals were aluminium-tagged, numbered and identified in situ and/or in the herbarium at the National Institute of Amazonian Research (INPA), Manaus, Brazil. Skilled INPA herbarium technicians with extensive field and herbarium experience from floristic inventories in the central-western Brazilian Amazon performed all identifications. Vouchers from 1174 individuals were collected and subsequently identified at the INPA herbarium to verify the accuracy of field identifications at the level of genus and species. Individuals that could not be determined to species level were sorted to morpho-species or, where applicable, higher taxonomic levels.

2.3. Data Analyses

To test for differences in woody plant stem density, dbh, basal area (BA), total height, height of first branching, branching depth and proportion of stem with branches in relation to total height, we first ran Shapiro–Wilk's tests of normality and compared the variances of terra firme and várzea using Fisher's F-test. For normally distributed data, we ran Student's two-sample *t*-tests where data conformed to homoscedasticity, or Welch two-sample *t*-tests where they did not. Where the data did not conform to normality, we ran independent two-group Wilcoxon–Mann–Whitney tests.

For each family and species, we calculated the relative density (Rel. Den.), relative dominance (Rel. Dom.), relative diversity (Rel. Div.) and relative frequency (Rel. Freq.). For formulas, see Appendix A. In addition, we calculated the Family Importance Value (FIV = ∑ Rel. Den. + Rel. Dom. + Rel. Div.) for each family [34] and the Importance Value Index (IVI = ∑ Rel. Dens + Rel. Dom. + Rel. Freq.) for each species [35].

We used the 'BiodiversityR' package version 2.11-1 [36] to calculate indices of species richness and diversity, and to produce species rarefaction curves estimating the expected number of additional species for every additional survey plot, in relation to the mean number of individuals per plot. Species rarefactions were based on 100 permutations.

To investigate the spatial variation in woody plant species composition, we used the 'vegan' package, version 2.5-5 [37]. We tested for spatial autocorrelation among plots using a partial Mantel test with a Bray-Curtis dissimilarity matrix for the woody plant species composition, and a Euclidian distance matrix for the geographic distances [37]. To assess variations in species composition, we used non-metric multidimensional scaling (NMDS) through the *metaMDS* function with the Bray-Curtis dissimilarity index. We used the *envfit* method to fit forest type (i.e., TF or VZ) onto the NMDS ordination as a measure of the correlation of forest type with the NMDS axes. Additionally, we performed a

permutational multivariate analysis of variance test (PERMANOVA) with forest type as predictor of the woody plant composition dissimilarity matrices, with the Bray-Curtis index as the response variable.

To analyse for multivariate homogeneity of group dispersions, we used the *betadisper* function in vegan. Analyses for multivariate homogeneity of group dispersions inform us how the variances within groups differ among groups [38]. Defining β-diversity as the variability in species composition among sampling units within groups, tests of multivariate homogeneity of group dispersions may thus inform us about differences in β-diversity between the two forest types [39]. To minimise the influence of the most abundant species on the multivariate dispersion analyses, we first square-root transformed the species abundance matrix [40]. To adjust for potential small sample bias in the analyses, we used the *bias.adjust* option of the *betadisper* function [40,41]. All analyses were run in R, version 3.5.2 [42].

3. Results

3.1. Forest Structure

In total, we recorded 4690 individual trees, 274 palms, 25 hemi-epiphytes and 450 lianas across both terra firme and várzea forests (*n* = 97 plots; 9.7 ha), yielding 5439 individuals or 5483 stems (Table 1). The dbh size class distributions in the two forest types show inverse J-shaped curves for both the combined tree and hemi-epiphyte assemblages and the lianas (Figure 2). For palms, the size class distribution was a sigmoid shape, showing a slight shift in climax towards larger diameters in várzea palms (20–25 cm dbh) compared to terra firme palms (15–20 cm dbh; Figure 2).

Table 1. Number of plots (Plots) and number of ha. (Ha.) inventoried in terra firme (TF) and várzea (VZ) forests along the Juruá River, western Brazilian Amazon. Number of stems (Stems), including hollow stems, and number of individuals (Inds.), including multi-stemmed individuals, are given as count data with percentiles in parentheses (%). Mean number of stems per plot (Plot mean) is given ± standard deviations (sd). Mean diameter at breast height (dbh) ± sd is in cm, basal area (BA) in m² and mean height ± sd in m. All values are given per growth form, forest type and for both forest types combined. Values refer to trees, palms and hemi-epiphytes (hemi-ep.) with dbh ≥ 10 cm and woody lianas ≥ 5 cm dbh. Total height in m is also given as overall minimum (Min), maximum (Max), median and mode values. Differences in stem density, dbh, plot BA and mean total height between várzea and terra firme for normally distributed data were tested with classic Student's two-sample *t*-tests where group variances were homogenous or Welch two-sample *t*-tests where group variances were heterogenous. Where data did not conform to normality, we used independent two-group Wilcoxon–Mann–Whitney tests. Asterisks in the table indicate significant results.

		TF	VZ	Total
	Plots	46	51	97
	Ha.	4.60	5.10	9.70
Stems	Trees (%)	2288 (89.80)	2443 (83.24)	4731 (86.28)
	Hemi-ep. (%)	5 (0.20)	22 (0.75)	27 (0.49)
	Palms (%)	104 (4.08)	170 (5.79)	274 (5.00)
	Lianas (%)	151 (5.93)	300 (10.22)	451 (8.23)
	Total (%)	2548 (100.00)	2935 (100.00)	5483 (100.00)
	Hollow (%)	34 (1.33)	63 (2.15)	97 (1.77)
	Plot mean ± sd	55.39 ± 11.07	57.55 ± 12.29	56.53 ± 11.72
Inds.	Trees (%)	2282 (89.77)	2408 (83.12)	4690 (86.23)
	Hemi-ep. (%)	5 (0.20)	20 (0.69)	25 (0.46)
	Palms (%)	104 (4.09)	170 (5.87)	274 (5.04)
	Lianas (%)	151 (5.94)	299 (10.32)	450 (8.27)
	Total (%)	2542 (100.00)	2897 (100.00)	5439 (100)
	Multi-stemmed (%)	4 (0.16)	30 (1.04)	34 (0.63)
Mean dbh ± sd, cm	Trees	21.85 ± 13.40	22.71 ± 16.09	22.29 ± 14.85
	Hemi-ep.	27.28 ± 9.36	44.05 ± 42.81	40.94 ± 39.22
	Palms ***	16.65 ± 4.60	22.93 ± 6.84	20.54 ± 6.80
	Lianas	8.48 ± 2.79	9.14 ± 4.04	8.92 ± 3.68
	Total	20.85 ± 13.17	21.50 ± 15.93	21.40 ± 14.71

Table 1. *Cont.*

		TF	VZ	Total
BA, m^2	Tree	118.03	148.59	266.62
	Hemi-ep.	0.32	6.38	6.70
	Palm	2.44	7.64	10.08
	Liana	0.94	2.35	3.29
	Total	121.73	164.96	286.69
	Plot mean ± sd *	2.65 ± 0.71	3.23 ± 1.18	2.96 ± 1.03
Mean height ± sd, m	Tree ***	20.16 ± 7.40	16.20 ± 7.71	18.12 ± 7.81
	Hemi-ep.	27.67 ± 8.74	24.30 ± 7.95	24.89 ± 7.92
	Palm	17.88 ± 5.94	16.90 ± 6.12	17.27 ± 6.06
	Overall ***	20.07 ± 7.36	16.29 ± 7.64	18.10 ± 7.74
Overall height, m	Min	3.00	1.70	1.70
	Max	50.00	47.37	50.00
	Median	19.00	15.00	16.43
	Mode	20.00	10.00	15.00

Significant difference between VZ and TF values at * $p < 0.05$ and *** $p < 0.001$.
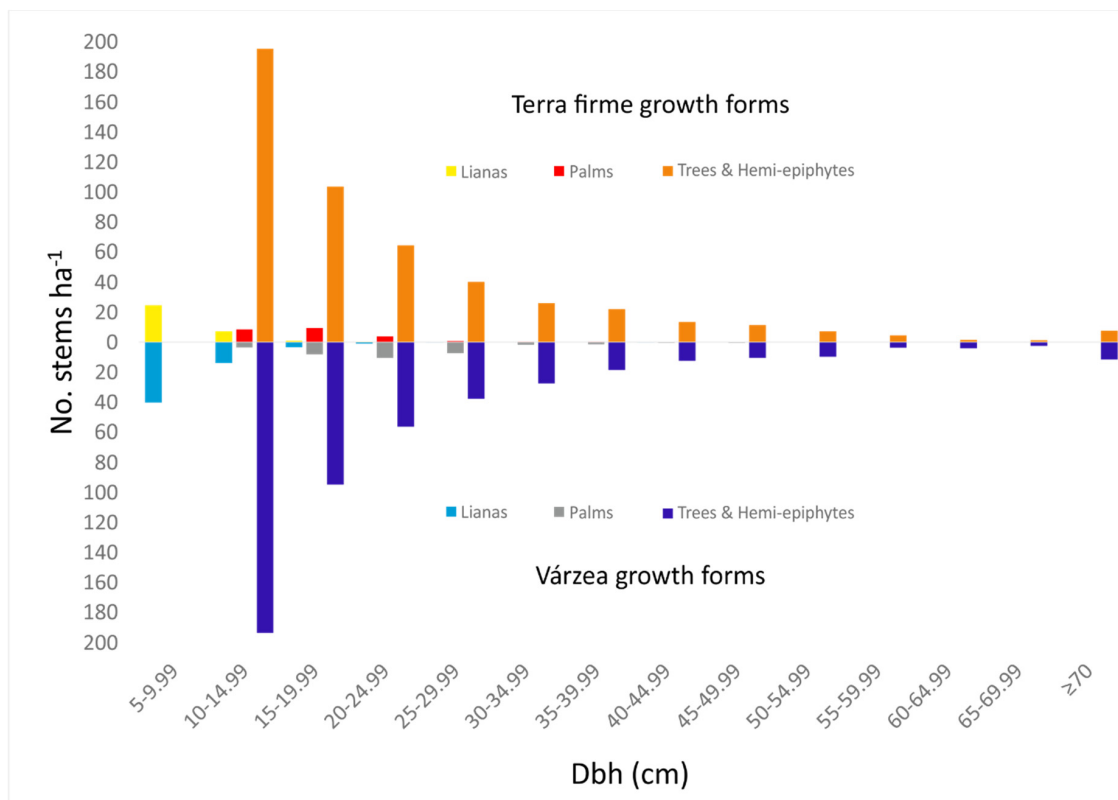

Figure 2. Number of stems per hectare across diameter at breast height (Dbh) size classes with five cm intervals where, e.g., 5–9.99 is from five cm dbh up to, but not including, 10 cm dbh. Values are given per growth form for terra firme (yellow = lianas, red = palms, orange = trees and hemi-epiphytes) and várzea (light blue = lianas, grey = palms, dark blue = trees and hemi-epiphytes) forests along the central reaches of the Juruá River, western Brazilian Amazon.

Smaller trees measuring <30 cm dbh dominated both forest types. These accounted for 72.8% of all inventoried individuals in terra firme (80.9% of all terra firme trees) and 66.4% of all individuals in seasonally inundated forest (79.1% of all várzea trees). Large trees (≥70 cm dbh) represented just 2.0% of all trees (1.5% and 2.4% of the TF and VZ trees, respectively), or 1.7% of all individuals (1.4% and 2.0% of the TF and VZ individuals, respectively). Only 18 (0.4%) trees in the entire sample attained

diameters greater than 100 cm dbh, two in terra firme and 16 in várzea. Six of these sixteen emergents were *Hura crepitans* (Euphorbiaceae) in várzea.

Mean total height was greater among terra firme woody plants compared to várzea (Wilcoxon–Mann–Whitney's W = 4,094,644, $p < 0.001$). However, when examining growth forms separately, only trees were significantly taller in terra firme compared to várzea (Wilcoxon–Mann–Whitney's W = 3,676,156, $p < 0.001$). There was no significant height difference between forest types for hemi-epiphytes or palms (Table 1). Palm dbh was significantly lower in terra firme compared to várzea (Wilcoxon–Mann–Whitney's W = 3739.5, $p < 0.001$; Table 1). There was no significant difference in dbh for trees, hemi-epiphytes or lianas. Terra firme had significantly lower basal area (Wilcoxon–Mann–Whitney's W = 818, *p*-value = 0.01) and fewer palms, hemi-epiphytes, lianas, hollow stems and multi-stemmed individuals compared to várzea (Table 1). The most frequently encountered multi-stemmed várzea species ($n = 5$) was *Theobroma cacao* (Malvaceae). The species most frequently encountered with hollow trunks were *Cecropia* species (VZ: $n = 19$, TF: $n = 16$). Várzea woody plants branched closer to the ground (Wilcoxon–Mann–Whitney's W = 3,520,973, $p < 0.001$), had greater branching depth (Wilcoxon–Mann–Whitney's W = 2,091,770, $p < 0.001$) and had branches along a greater portion of their stems, compared to terra firme trees and hemi-epiphytes (Wilcoxon–Mann–Whitney's W = 1,392,508, $p < 0.001$).

3.2. Floristic Diversity

In total, 931 species were recorded in the lowland terra firme and várzea forests combined (Table 2). Of these, 625 species occurred in terra firme and 526 in várzea (Table 2). Two hundred and twenty species (23.6%) were shared among terra firme and várzea forests, comprising 44.4% of all individuals. However, most species were unique to either terra firme (43.5%; Table 2) or várzea (32.9%; Table 2) and many species occurred only in a single plot (TF: 45.6%, $n = 285$; VZ: 42.2%, $n = 222$). Most of the shared species were rare and occurred with few observations in one forest type and single observations in the other (69.5%, $n = 153$), or as singletons in both forest types (13.2%, $n = 29$). Only 44 (20.0%) of the 220 shared species had 10 or more individuals recorded in at least one forest type. Three species (1.4%) had 10 or more individuals recorded in both forest types. Although the species rarefaction curves clearly indicate a greater species richness in terra firme compared to várzea, the curves did not reach an asymptote for either forest type (Figure 3).

Table 2. Number of species (Spp.), number of genera (Gen.) and number of families (Fam.) found within the terra firme (TF) and várzea (VZ) forests along the Juruá River, western Brazilian Amazon. Values are given as counts per growth form, forest type and for both forest types combined, with percentiles of individuals not identified to each taxonomic level in parentheses (N/A, %). In addition, the numbers of Spp., Gen. and Fam. that were unique to either forest type (Unique) or occurred as singletons in either or both forest types (Singleton) are given as counts and percentiles in parenthesis (%). All values refer to trees, palms and hemi-epiphytes (hemi-ep.) with dbh ≥ 10 cm and woody lianas ≥ 5 cm dbh.

		TF	VZ	Total
Spp.	Trees (N/A, %)	576 (4.08)	466 (4.98)	847 (4.54)
	Hemi-ep. (N/A, %)	3 (0.00)	9 (5.00)	11 (4.00)
	Palms (N/A, %)	7 (4.81)	5 (0.00)	9 (1.82)
	Lianas (N/A, %)	41 (29.80)	58 (21.74)	79 (24.44)
	Total (N/A, %)	625 (5.63)	526 (6.42)	931 (6.05)
	Unique (%)	405 (43.50)	306 (32.87)	711 (76.37)
	Singleton (%)	285 (45.60)	222 (42.21)	314 (33.73)
Gen.	Trees (N/A, %)	214 (2.50)	188 (1.00)	273 (1.73)
	Hemi-ep. (N/A, %)	2 (0.00)	2 (0.00)	2 (0.00)
	Palms (N/A, %)	7 (3.85)	4 (0.00)	7 (1.46)

Table 2. *Cont.*

		TF	VZ	Total
	Lianas (N/A, %)	31 (23.18)	45 (14.72)	54 (17.56)
	Total (N/A, %)	247 (3.78)	226 (2.35)	317 (3.02)
	Unique (%)	91 (28.71)	70 (22.08)	161 (50.79)
	Singleton (%)	66 (26.72)	42 (18.58)	56 (17.67)
Fam.	Trees (N/A, %)	63 (1.97)	53 (0.58)	67 (1.26)
	Hemi-ep. (N/A, %)	2 (0.00)	2 (0.00)	2 (0.00)
	Palms (N/A, %)	1 (0.00)	1 (0.00)	1 (0.00)
	Lianas (N/A, %)	17 (17.88)	23 (12.71)	28 (14.44)
	Total (N/A, %)	69 (2.83)	63 (1.79)	77 (2.28)
	Unique (%)	14 (18.18)	8 (10.39)	22 (28.57)
	Singleton (%)	9 (13.04)	4 (6.35)	6 (7.79)
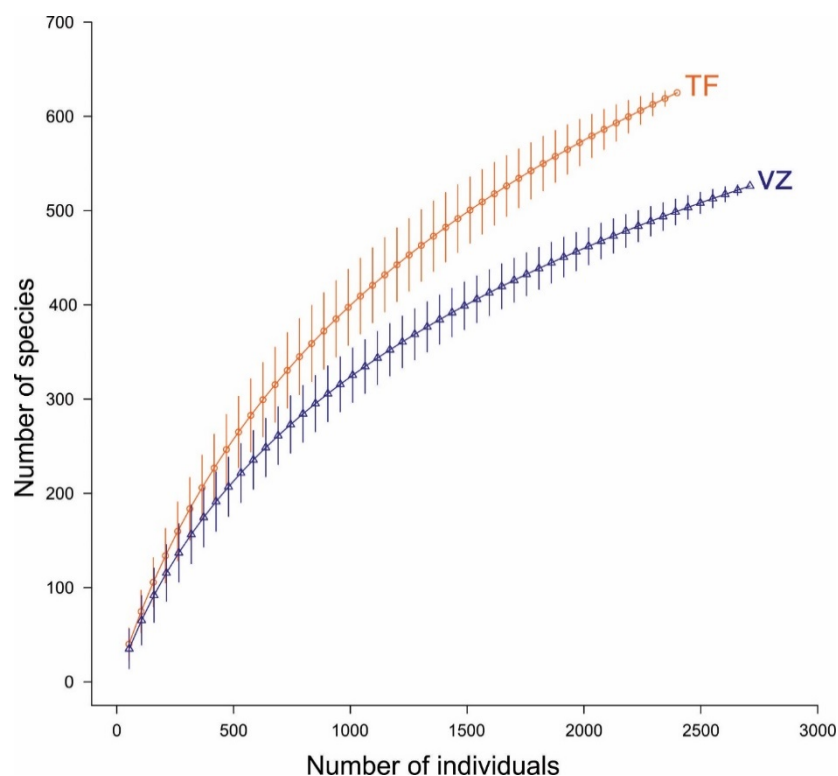
Figure 3. Sample-based rarefaction curves, scaled by the number of pooled individuals per survey plot (sample) for terra firme forest (TF, in orange) and várzea forest (VZ, in blue). The bars indicate ±2 standard deviations.

3.3. Family Importance Value

Leguminosae (Fabaceae) dominated the family importance value (FIV) in both forest types, mainly because of the large number of species in this super-family (TF: FIV = 40.93; 15.7%; VZ: FIV = 38.98; 13.9%; Table 3; Table 4). In both forest types, Lecythidaceae was the second most important family, followed by Sapotaceae. In terra firme, Lecythidaceae represented both the highest number of individuals (*n* = 383) and the greatest basal area (BA) (Table 3). In várzea, Lecythidaceae was the second most dominant family, Sapotaceae was the second most species-rich family and Annonaceae was the second most abundant family (Table 4). The full FIV list for all families is presented in Supplementary Table S1.

Table 3. The ten most important families in lowland terra firme, listed in descending order of family importance value (FIV). Values are based on all woody plants with species identifications. The number of individuals (No. Inds.) and the number of species within each family (No. Spp.) are given as counts. Basal area (BA) in m^2. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative diversity (Rel. Div.) are given as percentages, where 100 equals 100% (Supplementary Table S1).

Family	No. Inds.	BA (m^2)	No. Spp.	Rel. Den.	Rel. Dom.	Rel. Div.	FIV
Leguminosae	286	16.12	98	11.58	13.67	15.68	40.93
Lecythidaceae	383	20.70	30	15.51	17.55	4.80	37.86
Sapotaceae	163	9.54	47	6.60	8.09	7.52	22.21
Chrysobalanaceae	186	9.61	33	7.53	8.15	5.28	20.96
Myristicaceae	203	8.49	21	8.22	7.20	3.36	18.78
Moraceae	134	8.68	31	5.43	7.36	4.96	17.75
Lauraceae	91	6.50	30	3.68	5.51	4.80	14.00
Burseraceae	114	3.03	34	4.62	2.57	5.44	12.62
Urticaceae	73	4.35	17	2.96	3.69	2.72	9.36
Malvaceae	89	2.26	21	3.60	1.92	3.36	8.88
Subtotal	1722	89.26	362	69.72	75.70	57.92	203.34
Remaining	748	28.65	263	30.28	24.30	42.08	96.66
Total	2470	117.91	625	100	100	100	300

Table 4. The ten most important várzea families listed in descending order of family importance value (FIV). Values are based on all woody plants with species identifications. The number of individuals (No. Inds.) and the number of species within each family (No. Spp.) are given as counts. Basal area (BA) in m^2. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative diversity (Rel. Div.) are given as percentages, where 100 equals 100% (Supplementary Table S1).

Family	No. Inds.	BA (m^2)	No. Spp.	Rel. Den.	Rel. Dom.	Rel. Div.	FIV
Leguminosae	357	20.46	73	12.55	12.55	13.88	38.98
Lecythidaceae	201	19.05	22	7.07	11.69	4.18	22.94
Sapotaceae	201	13.66	38	7.07	8.38	7.22	22.67
Annonaceae	279	8.70	35	9.81	5.34	6.65	21.80
Euphorbiaceae	138	17.05	22	4.85	10.46	4.18	19.50
Malvaceae	134	9.16	24	4.71	5.62	4.56	14.89
Arecaceae	170	7.64	5	5.98	4.69	0.95	11.61
Urticaceae	65	8.21	15	2.28	5.04	2.85	10.18
Myristicaceae	107	7.66	8	3.76	4.70	1.52	9.98
Moraceae	64	4.15	22	2.25	2.55	4.18	8.98
Subtotal	1716	115.75	264	60.32	71.01	50.19	181.51
Remaining	1129	47.26	262	39.68	28.99	49.81	118.49
Total	2845	163.01	526	100	100	100	300

3.4. Species Importance Value Index

Three *Eschweilera* spp. (Lecythidaceae) top the terra firme Importance Value Index (IVI). Of these, *Eschweilera coriacea* was the most important, largely due to the high basal area derived from its large stems and high abundance (Table 5). In várzea, *Hura crepitans* (Euphorbiaceae) was the most important tree species and dominated the basal area, despite its relatively low abundance (Table 6). Palms (Arecaceae) were abundant in both forest types and both *Euterpe precatoria* (TF) and *Astrocaryum jauari* (VZ) were among the most important species. None of the 10 most important species were shared between terra firme and várzea. The IVI for all species is presented in Supplementary Table S2.

Table 5. The ten most important species in lowland terra firme, listed in descending order of Importance Value Index (IVI). Values are based on all woody plants with species identifications. Growth forms (G.F.) observed for each species are given as t = tree, l = liana and p = palm. The number of individuals within each species (No. Inds.) and the number of plots in which each species occurs (Plot occ.) are given as counts. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative frequency (Rel. Freq.) are given as percentages, where 100 equals 100% (Supplementary Table S2).

No.	Species	Family	G.F.	No. Inds.	BA (m^2)	Plot occ.	Rel. Den.	Rel. Dom.	Rel. Freq.	IVI
1	*Eschweilera coriacea* (DC.) S.A.Mori	Lecythidaceae	t, l	87	4.13	33	3.63	3.58	1.79	8.99
2	*Eschweilera wachenheimii* (Benoist) Sandwith	Lecythidaceae	t	103	3.11	36	4.29	2.69	1.95	8.94
3	*Eschweilera truncata* A.C.Sm.	Lecythidaceae	t	59	3.20	18	2.46	2.77	0.98	6.21
4	*Euterpe precatoria* Mart.	Arecaceae	p	55	1.07	17	2.29	0.93	0.92	4.14
5	*Eschweilera grandiflora* (Aubl.) Sandwith	Lecythidaceae	t	37	1.80	18	1.54	1.56	0.98	4.08
6	*Osteophloeum platyspermum* (Spruce ex A.DC.) Warb.	Myristicaceae	t	23	2.34	17	0.96	2.03	0.92	3.91
7	*Pouteria guianensis* Aubl.	Sapotaceae	t	30	1.74	20	1.25	1.50	1.09	3.84
8	*Iryanthera hostmannii* (Benth.) Warb.	Myristicaceae	t	36	1.34	21	1.50	1.16	1.14	3.80
9	*Cariniana micrantha* Ducke	Lecythidaceae	t	10	3.27	9	0.42	2.83	0.49	3.73
10	*Brosimum rubescens* Taub.	Moraceae	t	15	2.26	13	0.63	1.95	0.71	3.29
10	Subtotal	-	-	455	24.26	202	18.97	20.99	10.97	50.92
615	Remaining	-	-	1944	91.30	1640	81.03	79.01	89.03	249.08
625	Grand total	-	-	2399	115.56	1842	100	100	100	300

Table 6. The ten most important várzea species, listed in descending order of Importance Value Index (IVI). Values are based on all woody plants with species identifications. Growth forms (G.F.) observed for each species are given as t = tree and p = palm. The number of individuals within each species (No. Inds.) and the number of plots in which each species occurs (Plot occ.) are given as counts. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative frequency (Rel. Freq.) are given as percentages, where 100 equals 100% (Supplementary Table S2).

No.	Species	Family	G.F.	No. Inds.	BA (m^2)	Plot occ.	Rel. Den.	Rel. Dom.	Rel. Freq.	IVI
1	*Hura crepitans* L.	Euphorbiaceae	t	14	11.68	9	0.52	7.47	0.50	8.49
2	*Virola surinamensis* (Rol. ex Rottb.) Warb.	Myristicaceae	t	56	5.98	26	2.07	3.83	1.45	7.34
3	*Eschweilera ovalifolia* (DC.) Nied.	Lecythidaceae	t	50	5.75	22	1.84	3.68	1.23	6.75
4	*Astrocaryum jauari* Mart.	Arecaceae	p	59	2.88	11	2.18	1.85	0.61	4.64
5	*Garcinia madruno* (Kunth) Hammel	Clusiaceae	t	57	1.61	20	2.10	1.03	1.12	4.25
6	*Tapura juruana* (Ule) Rizzini	Dichapetalaceae	t	32	2.66	22	1.18	1.70	1.23	4.11
7	*Leonia glycycarpa* Ruiz & Pav.	Violaceae	t	44	1.60	25	1.62	1.02	1.39	4.04
8	*Eschweilera parviflora* (Aubl.) Miers	Lecythidaceae	t	35	2.65	18	1.29	1.70	1.00	3.99
9	*Pouteria glomerata* (Miq.) Radlk.	Sapotaceae	t	39	2.08	19	1.44	1.33	1.06	3.83
10	*Himatanthus sucuuba* (Spruce ex Müll.Arg.) Woodson	Apocynaceae	t	38	2.12	19	1.40	1.36	1.06	3.82
10	Subtotal	-	-	424	39.02	191	15.64	24.96	10.65	51.26
516	Remaining	-	-	2287	117.29	1602	84.36	75.04	89.35	248.74
526	Grand total	-	-	2711	156.31	1793	100	100	100	300

3.5. Community Composition

Overall dissimilarity in species composition was high among plots. Only four between-plot Bray-Curtis dissimilarities were below 60%, all within várzea. The lowest recorded Bray-Curtis dissimilarity between forest types was 79.6% (Supplementary Table S3). No species occurred in all plots of either forest type and only two species occurred in more than half of the terra firme plots: *Eschweilera wachenheimii* (Lecythidaceae; *n* = 36) and *Eschweilera coriacea* (Lecythidaceae; *n* = 33). Despite a lower total species richness in várzea, only *Virola surinamensis* (Myristicaceae) occurred in at least half of the várzea plots (*n* = 26).

We found greater resemblance in species composition among plots within the same forest type than when comparing plots between forest types (*envfit*: R^2 = 0.59, *p* < 0.001; PERMANOVA: R^2 = 0.11, F = 11.27, *p* = 0.001; Figure 4), although there was spatial autocorrelation between plots (Mantel test: r = 0.19, *p* = 0.001). Multivariate dispersion of inventory plots indicates that neither várzea nor terra firme plots are more clustered around their respective multivariate means than the other (*betadisper*: F = 0.30, N.Perm = 99, *p* = 0.57). Thus, both forest types show a similar variation in species composition among plots.
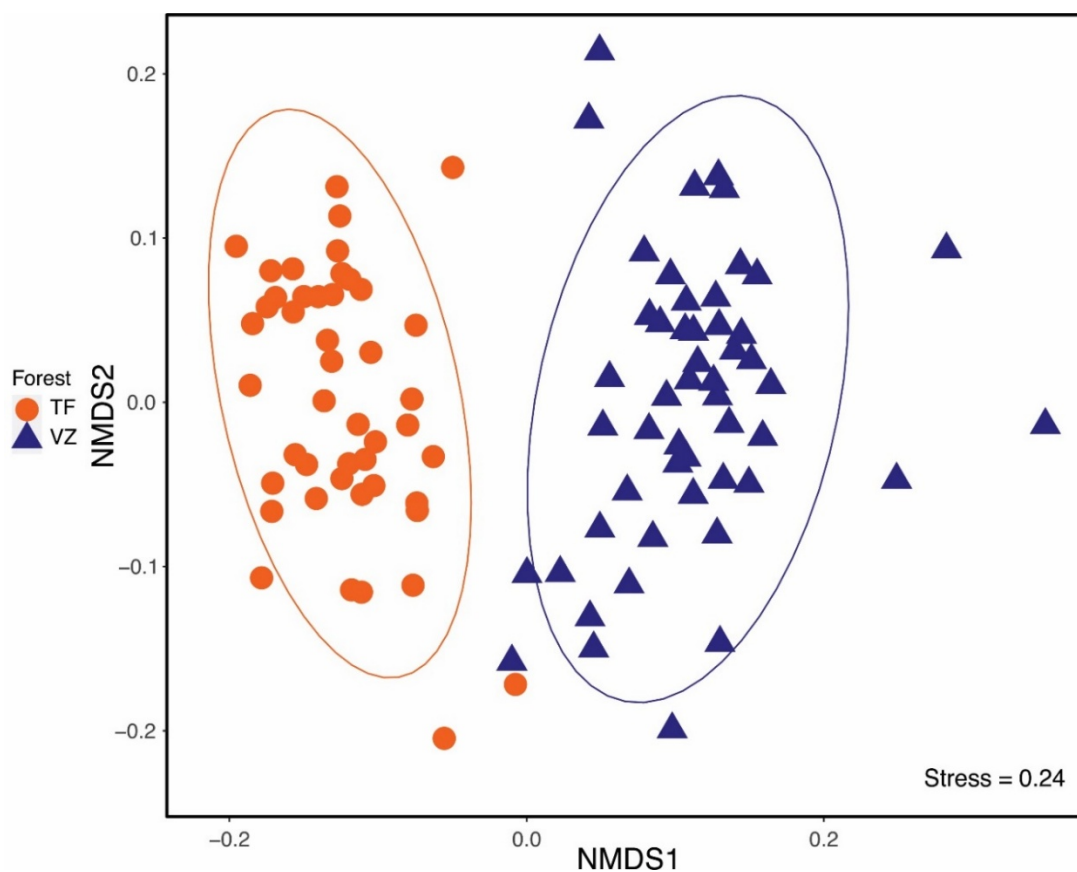
Figure 4. Non-metric multidimensional scaling (NMDS) ordination showing the relative position of inventory plots in terra firme forest (orange circles) and várzea forests (dark blue triangles), along axes NMDS1 and NMDS2. Ellipses represent 95% confidence intervals (CI) around group centroids. Plot positions within ordination space are based on Bray-Curtis dissimilarities. The stress measure indicates similarity of observed distance to ordination distance.

4. Discussion

4.1. Forest Structure

As seen from the high number of late-successional species characteristic of the central Juruá and the different strata that these represent, our inventory is typical of structurally intact and late-successional forests [43–45]. Both the terra firme and várzea forests of the central Juruá had well-stratified canopies featuring emergent trees of up to ca. 50 and 47 m, respectively.

The várzea forest had a greater diversity in growth forms than terra firme, and more multi-stemmed or hollow individuals. This may reflect the differences in disturbance regimes between the two forest types, with higher levels of disturbance in várzea forests driven by the impact of seasonal floods and their proximity to the Juruá River. For example, woody lianas typically occur in disturbed areas, such as secondary forests or forest edges [46,47]. In structurally intact terra firme forests, lianas are likely to become dominant only in treefall gaps [47], whereas with both natural clearings and the river margin, the propensity of edge habitat is considerably larger in structurally intact várzea forests. Similarly, the high number of hollow individuals that we observed in várzea forest was mostly driven by pioneer species typical of disturbed floodplain habitat, such as *Cecropia* spp. [48–50]. Moreover, since palms are associated with highly dynamic forests on weakly structured and nutrient-rich soils [51–53], the higher frequency and size of palms recorded in várzea may further reflect the influence of flooding on substrate properties and forest dynamics.

Both the terra firme and várzea forests had similar stem densities and high proportions of smaller trees (i.e., 10–30 cm dbh). However, trees grew taller in terra firme, whereas BA and degree of branching were significantly higher in várzea. These structural differences between terra firme and várzea woody plants may result from differences in forest dynamics and substrate fertility. High seasonality and substrate fertility in várzea might cause trees to grow quicker or better during favourable times of the year (i.e., dynamic growth in response to the changing environment) [54], thus supporting higher BA but potentially lighter wood density [55]. In contrast, less seasonal variability and lower substrate fertility in terra firme may cause woody plants to grow slower, but more evenly, throughout the year. Slow lateral growth results in more structural matter per unit volume wood, and thus greater stability, supportive of higher stems [56].

Structural and functional differences between forest types interact to determine the amount of standing, living woody biomass across the forest landscape. Therefore, the higher BA and degree of branching in várzea woody plants is potentially counterbalanced by taller terra firme stems, plus previous findings from the same region which show that terra firme trees store more carbon per unit volume than várzea conspecifics [57]. Hence, both várzea and terra firme may produce similar amounts of standing, live woody biomass in the Juruá. This would compare to a case from the southern Amazon where dry season length and storm frequency affected stem density and individual biomass of trees and palms differently across two forest types but resulted in similar forest biomass due to complementary responses in structural variables to these environmental stresses [58].

4.2. Floristic Composition and Diversity

In the Juruá, almost one quarter of all woody plant species (23.6%) occurred in both terra firme and várzea. Our findings thus support previous reports of several shared species among terra firme and seasonally flooded forests [29,59]. However, most of these occurred predominantly in one forest type or as singletons in both forest types. This could indicate that many of the shared species are generally rare within the forest matrix or represent outlier observations of individuals in one of the forest types where they would straddle the extremes of their environmental tolerance limits [60–63]. Thus, we see that differences in environmental stress, e.g., seasonal flooding versus no seasonal flooding, between várzea and terra firme forests limit species distributions and cause the woody plant communities to shift. The great dissimilarity in species composition among várzea forest plots may result from the diversity of microhabitats and successional stages they cover along the

hydro-topographic gradient [29,43]. This variability in species composition contributed to a high total species richness. The species rarefactions suggest that the central Juruá várzeas are some of the most species-rich floodplains in the Amazon [24,64].

Amazonian terra firme forests are well-documented to be more species-rich than seasonally flooded forests [17]. This is supported by our study, where terra firme displayed a higher total species richness than the várzea forest. At the Amazon basin-wide scale, the greater diversity in terra firme woody plants is attributed to habitat availability (terra firme comprises ca. 87% of available forest habitat in the Amazon compared to ca. 13% forested floodplain habitat) [3,65], habitat stability [66], a diversity in climatic and edaphic conditions [67–70] and the evolutionary dynamics of land formations, e.g., through processes that undo or induce dispersal barriers and subsequent speciation [71]. At local scales, a higher diversity in terra firme woody plant communities compared to its floodplain counterpart may also be attributed to a greater stability and longer history. Terra firme habitat has been available for colonisation by woody plants for much longer than present várzea habitat. Moreover, even at this local scale, the rate of disturbance in the terra firme is much lower compared to the várzea, where forest habitat is formed and eroded on a dynamic, seasonal basis [43,72]. Given these different drivers of woody plant diversification across seasonally flooded and terra firme forests, it is perhaps not surprising that terra firme and várzea forests in the Juruá showed similar levels of variation in species composition among plots around their respective multivariate means (i.e., similar β-diversities).

4.3. Important Families and Species

In accordance with previous work from central Amazonia, Leguminosae (Fabaceae), Lecythidaceae, Sapotaceae and Myristicaceae were among the most important families in both terra firme and várzea forests [73–75]. For other Amazonian regions, however, these families may be considerably less common. As an example, Lecythidaceae is much less important in terra firme forests of western (e.g., References [76–78]) and eastern Amazonia (e.g., References [79,80]). Our survey further corroborates the importance of Chrysobalanaceae and Moraceae in terra firme forests [73–75] and of Annonaceae and Euphorbiaceae in várzea forests [6,59,79,81]. Additionally, palms constitute an important part of both the Juruá and Amazonian arborescent flora.

A recent study found that six of the ten most common Amazonian arborescent species were palms [82]. In the Juruá, palms contributed 4%–6% of the inventoried individuals and 2%–5% of the total BA in the terra firme and várzea forests, respectively. *Euterpe precatoria*, potentially the most common woody species across the entire Amazon [83], was the most prominent terra firme palm species for the Juruá, where it was twice as common and more widespread than in várzea. *Astrocaryum jauari* was the most important várzea palm species. Overall, however, *Eschweilera* tree species were particularly prominent in the terra firme forest and *Eschweilera coriacea* was the most common tree, both for the Juruá and the Amazon at large [82]. *Hura crepitans* (Euphorbiaceae) was the most important floodplain species. In fact, *Hura crepitans*, as well as *Virola surinamensis* (Myristicaceae), the second most important várzea species in the Juruá, are both scarce in many floodplain areas across the Amazon basin due to logging [84,85]. Their importance in the central Juruá may therefore reflect the protected status of these floodplains [86].

Together, the most conspicuous woody plant species of the Juruá represented the entire terra firme and várzea canopy strata. In terra firme, *Cariniana micrantha* is an emergent tree, *Eschweilera coriacea*, *Eschweilera truncata* and *Euterpe precatoria* are common upper-canopy features, *Brosimum rubescens* occurs mid- to upper-canopy, *Osteophloeum platyspermum* grows mid-canopy and *Eschweilera grandiflora*, *Iryanthera hostmannii* and *Eschweilera wachenheimii* feature in the understorey [87–90]. In várzea, *Hura crepitans* and *Virola surinamensis* are upper-canopy to emergent trees, *Astrocaryum jauari* and *Eschweilera parviflora* grow in the upper canopy, *Tapura juruana*, *Pouteria glomerata*, *Himatanthus sucuuba*, *Pouteria procera* and *Leonia glycycarpa* occur mid-canopy, and *Theobroma cacao* grows in the understorey [91]. Except for *Pouteria glomerata*, a late-secondary forest species, the other characteristic várzea species are late-successional species [91].

5. Conclusions

Rare or sparsely distributed species drive most of the woody plant diversity in both low-lying terra firme forests on paleo-várzea sediments and seasonally flooded várzea forests on the floodplain of the central Juruá River basin. Both terra firme and várzea show high variation in plot-level species composition, demonstrating heterogeneity within forest types, even at small spatial scales. Although species richness was highest in terra firme, the Juruá várzea forest contain more woody species than most inventories have recorded for Amazonian floodplain forests. Given the high species turnover across terra firme and várzea, floodplain forests are clearly an important complement to terra firme woody plant diversity. The high proportion of singleton observations and forest type specialists in the central Juruá highlight the need for further floristic inventories from a wider range of geographically remote areas if we are to discover and properly describe the Amazonian flora. As a step in that direction, this study helps address the patchy botanical records of sparsely distributed Amazonian woody species.

Appendix A

Formulas for calculating (a) relative density (Rel. Den.), (b) relative dominance (Rel. Dom.), (c) relative diversity (Rel. Div.) and (d) relative frequency (Rel. Freq.).

$$(a)\ \text{Rel.Den.} = \frac{\text{No. of individuals of a family or species} \times 100}{\text{Total no. of individuals in sample}}$$

$$(b)\ \text{Rel.Dom.} = \frac{\text{Basal area of a family or species} \times 100}{\text{Total basal area in sample}}$$

$$(c)\ \text{Rel.Div.} = \frac{\text{No. of species in a family} \times 100}{\text{Total no. of species}}$$

$$(d)\ \text{Rel.Freq.} = \frac{\text{Sampling units containing a species} \times 100}{\text{Sum of all frequencies}}$$

References

1. Prance, G.T. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Philos. Trans. R. Soc. B Biol. Sci.* **1994**, *345*, 89–99. [CrossRef]
2. Gentry, A.H. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* **1988**, *75*, 1–34. [CrossRef]
3. Ter Steege, H.; De Oliveira, S.M.; Pitman, N.; Sabatier, D.; Antonelli, A.; Andino, J.E.G.; Aymard, G.A.; Salomão, R.P. Towards a dynamic list of Amazonian tree species. *Sci. Rep.* **2019**, *9*, 1–5. [CrossRef] [PubMed]
4. Cardoso, D.; Särkinen, T.; Alexander, S.; Amorim, A.M.; Bittrich, V.; Celis, M.; Daly, D.C.; Fiaschi, P.; Funk, V.A.; Giacomin, L.L.; et al. Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 10695–10700. [CrossRef] [PubMed]
5. Feeley, K.J. Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. *PLoS ONE* **2015**, *10*, e0125629. [CrossRef] [PubMed]
6. Luize, B.G.; Magalhães, J.L.L.; Queiroz, H.; Lopes, M.A.; Venticinque, E.M.; de Moraes Novo, E.M.L.; Silva, T.S.F. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? *PLoS ONE* **2018**, *13*, e0198130. [CrossRef]
7. Hopkins, M.J.G. Are we close to knowing the plant diversity of the Amazon? *An. Acad. Bras. Ciênc.* **2018**, *91*, e20190396. [CrossRef]
8. Hopkins, M.J.G. Modelling the known and unknown plant biodiversity of the Amazon basin. *J. Biogeogr.* **2007**, *34*, 1400–1411. [CrossRef]
9. Wallace, A.R. *A Narrative of Travels on the Amazon and Rio Negro*; Ward, Lock: London, UK, 1853; p. 541.
10. Kalamandeen, M.; Gloor, E.; Mitchard, E.T.A.; Quincey, D.; Ziv, G.; Spracklen, D.; Spracklen, B.; Adami, M.; Aragão, L.; Galbraith, D. Pervasive rise of small-scale deforestation in Amazonia. *Sci. Rep.* **2018**, *8*, 1600. [CrossRef]
11. Aragão, L.E.O.C.; Malhi, Y.; Barbier, N.; Lima, A.; Shimabukuro, Y.; Anderson, L.; Saatchi, S. Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philos. Trans. R. Soc. B Biol. Sci.* **2008**, *363*, 1779–1785. [CrossRef]
12. Souza, J.C.M.; Kirchhoff, F.T.; Oliveira, B.C.; Ribeiro, J.G.; Sales, M.H. Long-term annual surface water change in the Brazilian Amazon biome: Potential links with deforestation, infrastructure development and climate change. *Water* **2019**, *11*, 566. [CrossRef]
13. de Area Leão Pereira, E.J.; Silveira Ferreira, P.J.; de Santana Ribeiro, L.C.; Sabadini Carvalho, T.; de Barros Pereira, H.B. Policy in Brazil (2016–2019) threaten conservation of the Amazon rainforest. *Environ. Sci. Policy* **2019**, *100*, 8–12. [CrossRef]
14. Esquivel-Muelbert, A.; Baker, T.R.; Dexter, K.G.; Lewis, S.L.; Brienen, R.J.W.; Feldpausch, T.R.; Lloyd, J.; Monteagudo-Mendoza, A.; Arroyo, L.; Álvarez-Dávila, E.; et al. Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* **2019**, *25*, 39–56. [CrossRef] [PubMed]
15. Costa, M.H.; Coe, M.T.; Guyot, J.L.; Batistella, M.; Artaxo, P.; Nobre, C.; Bustamante, M.; Luizao, F.J. Effects of climatic variability and deforestation on surface water regimes. In *Sea Ice*; American Geophysical Union (AGU): Washington, DC, USA, 2009; pp. 543–553.
16. Hilker, T.; Lyapustin, A.I.; Tucker, C.J.; Hall, F.G.; Myneni, R.B.; Wang, Y.; Bi, J.; De Moura, Y.M.; Sellers, P.J. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 16041–16046. [CrossRef] [PubMed]
17. Wittmann, F.; Marques, M.C.M.; Júnior, G.D.; Budke, J.C.; Piedade, M.T.F.; Wittmann, A.D.O.; Montero, J.C.; De Assis, R.L.; Targhetta, N.; Parolin, P.; et al. The Brazilian freshwater wetscape: Changes in tree community diversity and composition on climatic and geographic gradients. *PLoS ONE* **2017**, *12*, e0175003. [CrossRef]
18. Aleixo, I.; Norris, D.; Hemerik, L.; Barbosa, A.; Prata, E.; Costa, F.; Poorter, L. Amazonian rainforest tree mortality driven by climate and functional traits. *Nat. Clim. Chang.* **2019**, *9*, 384–388. [CrossRef]
19. Aragão, L.E.O.C.; Poulter, B.; Barlow, J.B.; Anderson, L.O.; Malhi, Y.; Saatchi, S.; Phillips, O.L.; Gloor, E. Environmental change and the carbon balance of Amazonian forests. *Biol. Rev.* **2014**, *89*, 913–931. [CrossRef]
20. Sombroek, W. *Amazon Soils, Wageningen*; Netherlands, Centre for Agricultural Publications and Documentation: Wageningen, The Netherlands, 1965.
21. Sombroek, W. Amazon landforms and soils in relation to biological diversity. *Acta Amaz.* **2000**, *30*, 81. [CrossRef]

22. Pires, J.M.; Prance, G.T. The vegetation types of the Brazilian Amazon. In *Key Environments: AMAZONIA*; Prance, G.T., Lovejoy, T.E., Eds.; Pergamon Press: Oxford, UK, 1985; pp. 109–145.

23. Parolin, P.; Ferreira, L.V.; Albernaz, A.L.K.; Almeida, S.S. Tree species distribution in Várzea forests of Brazilian Amazonia. *Folia Geobot. Phytotaxon.* **2004**, *39*, 371–383. [CrossRef]

24. Junk, W.J.; Piedade, M.T.F. An introduction to South American wetland forests: Distribution, definitions and general characterization. In *Forest-Water Interactions*; Springer Science and Business Media LLC: Berlin, Germany, 2010; pp. 3–25.

25. Räsänen, M.E.; Salo, J.S.; Kalliola, R.J. Fluvial perturbation in the western Amazon basin: Regulation by long-term Sub-Andean tectonics. *Science* **1987**, *238*, 1398–1401. [CrossRef]

26. Irion, G. Soil infertility in the Amazonian rain forest. *Naturwissenschaften* **1978**, *65*, 515–519. [CrossRef]

27. Furch, K.; Klinge, H. Chemical relationship between vegetation, soil and water in contrasting inundation areas of Amazonia. In *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*; Proctor, J., Ed.; Blackwell Scientific Publications: Oxford, UK, 1989; pp. 189–204. ISBN 0-632-02559-X.

28. Furch, K.; Junk, W.J. Physiochemical conditions in the floodplains. In *The Central Amazon Floodplain: Ecology of a Pulsing System*; Junk, W.J., Ed.; Springer: Berlin, Germany, 1997; pp. 69–108. ISBN 978-3-642-08214-6.

29. Wittmann, F.; Schongart, J.; Montero, J.C.; Motzer, T.; Junk, W.J.; Piedade, M.T.F.; Queiroz, H.L.; Worbes, M. Tree species composition and diversity gradients in white-water forests across the Amazon basin. *J. Biogeogr.* **2006**, *33*, 1334–1347. [CrossRef]

30. Normand, S.; Vormisto, J.; Svenning, J.; Grández, C.; Balslev, H. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecol.* **2006**, *186*, 161–176. [CrossRef]

31. Hawes, J.E.; Peres, C.A. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. *Biotropica* **2016**, *48*, 465–475. [CrossRef]

32. GADM Database. 2015. Available online: www.gadm.org (accessed on 4 May 2020).

33. *HAGLÖF SWEDEN AB Vertex IV and Transponder T3 Manual January 2007, v.1.0*; Haglöf Sweden AB: Långsele, Sweden, 2007; pp. 1–27.

34. Mori, S.A.; Boom, B.M.; De Carvalino, A.M.; Dos Santos, T.S. Ecological importance of Myrtaceae in an eastern Brazilian wet forest. *Biotropica* **1983**, *15*, 68. [CrossRef]

35. Worbes, M.; Klinge, H.; Revilla, J.D.; Martius, C. On the dynamics, floristic subdivision and geographical distribution of várzea forests in central Amazonia. *J. Veg. Sci.* **1992**, *3*, 553–564. [CrossRef]

36. Kindt, R.; Coe, R. *Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*; World Agroforestry Centre (ICRAF): Nairobi, Kenya, 2005; ISBN 92-9059-179-X.

37. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; et al. *Vegan: Community Ecology Package*; R Package, 2019; Available online: https://CRAN.R-project.org/package=vegan (accessed on 4 May 2020).

38. Anderson, M.J. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **2005**, *62*, 245–253. [CrossRef]

39. Anderson, M.J.; Ellingsen, K.E.; McArdle, B.H. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* **2006**, *9*, 683–693. [CrossRef]

40. Stier, A.; Geange, S.W.; Hanson, K.M.; Bolker, B.M. Predator density and timing of arrival affect reef fish community assembly. *Ecology* **2013**, *94*, 1057–1068. [CrossRef]

41. O'Neill, M.E.; Mathews, K.L. A weighted least squares approach to Levene's test of homogeneity of variance. *Aust. N. Z. J. Stat.* **2000**, *42*, 81–100. [CrossRef]

42. R Environment R Core Team. *R: A Language and Environment for Statistical Computing*; R Environment R Core Team, 2018; Available online: https://www.r-project.org/ (accessed on 4 May 2020).

43. Wittmann, A.D.O.; Schöngart, J.; Junk, W.J. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In *Forest-Water Interactions*; Springer Science and Business Media LLC: Berlin, Germany, 2010; pp. 61–102.

44. Montgomery, R.A.; Chazdon, R.L. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* **2001**, *82*, 2707–2718. [CrossRef]

45. Myster, R.W. The physical structure of forests in the Amazon basin: A review. *Bot. Rev.* **2016**, *82*, 407–427. [CrossRef]

46. Laurance, W.F.; Pérez-Salicrup, D.; Delamônica, P.; Fearnside, P.M.; D'Angelo, S.; Jerozolinski, A.; Pohl, L.; Lovejoy, T.E. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **2001**, *82*, 105–116. [CrossRef]

47. Campbell, M.J.; Magrach, A.; Laurance, S. Liana diversity and the future of tropical forests. In *Sustainable Development and Biodiversity*; Springer Science and Business Media LLC: Berlin, Germany, 2015; Volume 5, pp. 255–274.

48. Gaglioti, A.L.; Aguiar, D.P.P. Cecropia in Flora do Brasil 2020 em construção. Available online: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB24951 (accessed on 4 September 2020).

49. Parolin, P.; Oliveira, A.C.; Piedade, M.T.F.; Wittmann, F.; Junk, W.J. Pioneer trees in Amazonian floodplains: Three key species form monospecific stands in different habitats. *Folia Geobot. Phytotaxon.* **2002**, *37*, 225–238. [CrossRef]

50. Parolin, P. Life history and environment of *Cecropia latiloba* in Amazonian floodplains. *Rev. Biol. Trop.* **2002**, *50*, 531–545.

51. De Castilho, C.V.; Magnusson, W.E.; De Araújo, R.N.O.; Luizão, R.C.; Luizão, F.J.; Lima, A.P.; Higuchi, N. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manag.* **2006**, *234*, 85–96. [CrossRef]

52. Emilio, T.; Quesada, C.A.; Costa, F.R.C.; Magnusson, W.E.; Schietti, J.; Feldpausch, T.R.; Brienen, R.J.W.; Baker, T.R.; Chave, J.; Álvarez, E.; et al. Soil physical conditions limit palm and tree basal area in Amazonian forests. *Plant Ecol. Divers.* **2013**, *7*, 215–229. [CrossRef]

53. Nebel, G.; Kvist, L.P.; Vanclay, J.K.; Christensen, H.; Freitas, L.; Ruíz, J. Structure and floristic composition of flood plain forests in the Peruvian Amazon. *For. Ecol. Manag.* **2001**, *150*, 27–57. [CrossRef]

54. Parolin, P. Radial gradients in wood specific gravity in trees of central Amazonian floodplains. *IAWA J.* **2002**, *23*, 449–457. [CrossRef]

55. Muller-Landau, H.C. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **2004**, *36*, 20. [CrossRef]

56. Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **2009**, *12*, 351–366. [CrossRef]

57. Bredin, Y.K.; Peres, C.A.; Haugaasen, T. Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass. *For. Ecol. Manag.* **2020**, *473*, 118297. [CrossRef]

58. Schietti, J.; Martins, D.; Emilio, T.; Souza, P.F.; Levis, C.; Baccaro, F.B.; Pinto, J.L.P.d.V.; Moulatlet, G.M.; Stark, S.C.; Sarmento, K.; et al. Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *J. Ecol.* **2016**, *104*, 1335–1346. [CrossRef]

59. de Jesus Veiga Carim, M.; Wittmann, F.K.; Piedade, M.T.F.; a Silva Guimarães, J.R.; de Cássia Leôncio Tostes, L. Composition, diversity, and structure of tidal "Várzea" and "Igapó" floodplain forests in eastern Amazonia, Brazil. *Braz. J. Bot.* **2016**, *40*, 115–124. [CrossRef]

60. Parolin, P.; De Simone, O.; Haase, K.; Waldhoff, D.; Rottenberger, S.; Kuhn, U.; Kesselmeier, J.; Kleiss, B.; Schmidt, W.; Pledade, M.T.F.; et al. Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *Bot. Rev.* **2004**, *70*, 357–380. [CrossRef]

61. Junk, W.J.; Piedade, M.T.F.; Schöngart, J.; Wittmann, F.; Parolin, P. (Eds.) Part II Ecological and ecophysiological aspects of Amazonian floodplain forests. In *Amazonian Floodplain Forests Ecophysiology, Biodiversity and Sustainable Management*; Springer: Berlin, Germany, 2010; pp. 105–313. ISBN 978-90-481-8724-9.

62. Parolin, P. Submerged in darkness: Adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Ann. Bot.* **2008**, *103*, 359–376. [CrossRef]

63. Parolin, P. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* **2001**, *128*, 326–335. [CrossRef]

64. Wittmann, F.; Anhuf, D.; Funk, W.J. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.* **2002**, *18*, 805–820. [CrossRef]

65. Hess, L. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. *Remote Sens. Environ.* **2003**, *87*, 404–428. [CrossRef]

66. Ter Steege, H. Contribution of current and historical processes to patterns of tree diversity and composition in the Amazon. In *Amazonia: Landscape and Species Evolution. A Look into the Past*; Hoorn, C., Wesselingh, F.P., Eds.; Wiley-Blackwell: Hoboken, NJ, USA, 2010; ISBN 9781444306408.

67. Quesada, C.A.; Lloyd, J.; Schwarz, M.; Patiño, S.; Baker, T.R.; Czimczik, C.; Fyllas, N.M.; Martinelli, L.; Nardoto, G.B.; Schmerler, J.; et al. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* **2010**, *7*, 1515–1541. [CrossRef]

68. Zuquim, G.; Costa, F.R.C.; Tuomisto, H.; Moulatlet, G.M.; Figueiredo, F.O.G. The importance of soils in predicting the future of plant habitat suitability in a tropical forest. *Plant Soil* **2019**, *450*, 151–170. [CrossRef]

69. 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. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nat. Cell Biol.* **2006**, *443*, 444–447. [CrossRef]

70. Quesada, C.A.; Phillips, O.L.; Schwarz, M.; Czimczik, C.I.; Baker, T.R.; Patiño, S.; Fyllas, N.M.; Hodnett, M.G.; Herrera, R.; Almeida, S.; et al. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **2012**, *9*, 2203–2246. [CrossRef]

71. Ruokolainen, K.; Moulatlet, G.M.; Zuquim, G.; Hoorn, C.; Tuomisto, H. Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. *Front. Biogeogr.* **2019**, *11*, e45046. [CrossRef]

72. Wittmann, F.; Junk, W.J.; Piedade, M.T. The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Manag.* **2004**, *196*, 199–212. [CrossRef]

73. Haugaasen, T.; Peres, C.A. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. *Acta Amaz.* **2006**, *36*, 25–35. [CrossRef]

74. Prance, G.T.; Rodrigues, W.A.; Da Silva, M.F. Inventário florestal de um hectare de mata de terra firme km 30 da Estrada Manaus-Itacoatiara. *Acta Amaz.* **1976**, *6*, 9–35. [CrossRef]

75. Lima Filho, D.A.; Matos, F.D.A.; Amaral, L.; Revilla, J.D.; Coelho, L.S.; Ramos, J.F.; Santos, J.L. Inventário florístico de floresta ombrófila densa de terra firme, na região do Rio Urucu-Amazonas, Brasil. *Acta Amaz.* **2001**, *31*, 565. [CrossRef]

76. Balslev, H.; Luteyn, J.L.; Øllgaard, B.; Holm-Nielsen, L.B. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* **1987**, *92*, 37–57.

77. Boom, B.M. A forest inventory in Amazonian Bolivia. *Biotropica* **1986**, *18*, 287. [CrossRef]

78. Faber-Langendoen, N.; Gentry, A.H. The structure and diversity of rain forests at Bajo Calima, Choco region, western Colombia. *Biotropica* **1991**, *23*, 2–11. [CrossRef]

79. Campbell, D.G.; Daly, D.C.; Prance, G.T.; Maciel, U.N. Quantitative ecological inventory of terra firme and varzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* **1986**, *38*, 369–393. [CrossRef]

80. Almeida, S.S.; Lisboa, P.L.B.; Silva, A.S.L. Diversidade florística de uma comunidade arbórea na estação científica 'Ferreira Penna', em Caxiuanã (Pará). *Bol. Mus. Para. Emílio Goeldi Sér. Bot.* **1993**, *9*, 93–128.

81. De Assis, R.; Wittmann, A.D.O.; Bredin, Y.K.; Schöngart, J.; Quesada, C.A.N.; Piedade, M.T.F.; Haugaasen, T. Above-ground woody biomass distribution in Amazonian floodplain forests: Effects of hydroperiod and substrate properties. *For. Ecol. Manag.* **2019**, *432*, 365–375. [CrossRef]

82. ter Steege, H.; Prado, P.I.; Lima, R.A.F.d.; Pos, E.; de Souza Coelho, L.; de Andrade Lima Filho, D.; Salomão, R.P.; Amaral, I.L.; de Almeida Matos, F.D.; Castilho, C.V.; et al. Biased-corrected richness estimates for the Amazonian tree flora. *Sci. Rep.* **2020**, *10*, 1–13. [CrossRef]

83. Peacock, J.; Cerón, C.E.; Aragão, L.E.O.C.; Réjou-Méchain, M.; Levis, C.; van der Hout, P.; van der Meer, P.J.; de Oliveira, E.A.; Huamantupa-Chuquimaco, I.; Laurance, S.G.W.; et al. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **2015**, *6*, 6857. [CrossRef]

84. Albernaz, A.K.M.; Ayres, J.M. Selective logging along the middle Solimoes River. *Adv. Econ. Bot.* **1999**, *13*, 135–151.

85. Marinho, T.A.D.S.; Piedade, M.T.F.; Wittmann, A.D.O. Distribution and population structure of four central Amazonian high-várzea timber species. *Wetl. Ecol. Manag.* **2010**, *18*, 665–677. [CrossRef]

86. Mesquita de Azevedo, L.A.; da Silva Cruz, F.A.; Dias, A.; Batista, G.; Jeanne, G.d.S.; de Amaral Carvalho, J.; Kasecker, T.; Santiago, H.C.; Lederman, M.R.; Bendezú Estupiñán, G.M.; et al. *Plano de gestão da reserva de desenvolvimento sustentável de Uacari. Management Plan, 222*; Governo do estado; Secretária de estado do meio ambiente e desenvolvimento sustentável; Centro estadual de unidades de conservação: Amazonas, Carauari, Brazil, 2010.

87. Menores, A.; Grande, R.; Reserva, N. Myristicaceae. In *Flora da Reserva Ducke: Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central*; Ribeiro, J.E.L.d.S., Hopkins, M.J.C., Virentini, A., Suthers, C.A., Costa, M.A.d.S., de Brito, J.M., de Souza, M.A.D., Martins, H.P., Lohmann, L.G., Assuncão, P.A.C.L., et al., Eds.; INPA: Manaus, Brazil, 1999; pp. 136–145.

88. Mundo, V. Lecythidaceae. In *Flora da Reserva Ducke: Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central*; Ribeiro, J.E.L.d.S., Hopkins, M.J.C., Virentini, A., Suthers, C.A., Costa, M.A.d.S., de Brito, J.M., de Souza, M.A.D., Martins, H.P., Lohmann, L.G., Assuncão, P.A.C.L., et al., Eds.; INPA: Manaus, Brazil, 1999; pp. 274–287. ISBN 13 9788521100119.

89. Puig, H.; Fabre, A. Survival and growth of *Iryanthera hostmannii* seedlings and juveniles in the tropical rainforest of French Guyana. *J. Trop. Ecol.* **1997**, *13*, 139–143. [CrossRef]

90. Marimon, B.S.; Felfili, J.M.; Haridasan, M. Studies in monodominant forests in eastern Mato Grosso, Brazil: I. A forest of *Brosimum rubescens* Taub. *Edinb. J. Bot.* **2001**, *58*, 123–137. [CrossRef]

91. Wittmann, F.; Schöngart, J.; De Brito, J.M.; de Oliveira Wittmann, A.; Fernandez Piedade, M.T.; Parolin, P.; Junk, W.J.W.J.; Guillaumet, J.-L.J.L. *Manual of Trees from Central Amazonian Várzea Floodplains*; Cohn-Haft, M., Kossmann Ferraz, I.D., Eds.; Editora INPA: Manaus, Brazil, 2010; ISBN 978-85-211-0067-6.