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BLACK-WATER FORESTS (IGAPÓ) VS. WHITE-WATER FORESTS (VÁRZEA) IN THE AMAZON: FLORISTICS AND PHYSICAL STRUCTURE

BOSQUES DE AGUA NEGRO (IGAPÓ) VS. BOSQUES DE AGUAS BLANCAS (VÁRZEA) EN LA AMAZONÍA: FLORÍSTICA Y ESTRUCTURA FÍSICA

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ABSTRACT

Flooded forests occur across the landscape of the Amazon basin and, because they are important to our shared human density, need further investigation. Here I use replicated plots to examine the floristics and physical structure of the two most common kinds of flooded forest-types in the Amazon. I set up four 50 m x 50 m forest plots in black-water forest (ig*apó*) in Peru and also in white-water forest (várzea) in Ecuador. I then sampled all trees in all plots at least 10 cm dbh for species, and then generated a variety of floristic and physical parameters. There was species variation among the plots within both forest-types, but little variation in physical structure. The four ig*apó* plots taken together (now 1 ha) had 16 families, 29 genera and 31 species with Fabaceae, the most common family of which also had the most genera and the most species. The four várzea plots taken together (now 1 ha) had 42 families, 91 genera and 159 species, with Fabaceae again the most common family which also had the most genera and the most species. There were only four species in common. In general the várzea plots had more stems, and more large stems (at least 40 cm dbh) than the ig*apó* plots, but mean stem size was very similar. Structural comparison to *terra firme 1 ha plots showed it had more stems, thicker stems and more above-ground biomass compared to either of these pooled 1 ha flooded plots. Finally all* study plots conformed to the reverse J stem size distribution pattern for all stems.

Keywords: Ecuador, LTER, P*eru, T*amshiyacu-Tahuayo, Tipitini, Yasuni.

RESUMEN

Los bosques inundados se producen a través del paisaje de la cuenca del Amazonas y, debido a que son importantes para nuestra densidad humana compartida, necesitan una mayor investigación. Aquí utilizo parcelas replicadas para examinar los florística y estructura física de los dos tipos más comunes de los bosques de tipo inundado de la Amazonia. He definido de cuatro parcelas forestales de 50 mx 50 m en los bosques de agua negro (igapó) en Perú y también en los bosques de aguas bravas (várzea) en Ecuador. Entonces probé todos los árboles en todas las parcelas de al menos 10 cm dap para las especies, y luego genero una variedad de parámetros florísticos y físicos. Estos fueron la variación de especies entre las parcelas dentro de los dos tipos de bosque, pero poca variación en la estructura física. Los cuatro parcelas de igapó en conjunto (ahora 1 ha) tenían 16 familias, 29 géneros y 31 especies con Fabaceae la familia más común que también tenía la mayor cantidad de géneros y la mayoría de las especies. Las cuatro parcelas de várzea en su conjunto (ahora 1 ha) tenían 42 familias, 91 géneros y 159 especies de Fabaceae, de nuevo, la familia más común que también tenía la mayor cantidad de géneros y la mayoría de las especies. Sólo había cuatro especies en común. En general las parcelas de várzea tenían más tallos y tallos más grandes (al menos 40 cm dap) que las parcelas de igapó, pero el promedio del tallo tamaño fue muy similar. La comparación estructural a *tierra firme* 1 ha parcelas mostró que tenía más tallos más gruesos tallos y más biomasa aérea en comparación con cualquiera de estos combinados 1 ha de parcelas inundadas. Finalmente todas las parcelas de estudio se ajustaban al patrón de distribución del tamaño del tallo J inverso para todos los tallos.

Palabras clave: Ecuador, LTER, Perú, Tamshiyacu-Tahuayo, Tipitini, Yasuni.

INTRODUCTION

The Amazon river originates in the foothills of the Andean Mountains of South America and runs east into the Atlantic Ocean. It drains many smaller rivers along the way creating a huge watershed — the Amazon basin — which is generally located below 100 m asl. Associated with this watershed is the largest continuous rainforest in the world, bounded to the north by the Guiana crystalline shield and to the south by the Brazilian crystalline shield (Pires & Prance 1985) marked at their edges by cataracts in the rivers. This Amazonian rainforest encompasses a landscape of over 6,000,000 km^2 (Walter 1973) and is the most productive (Daly & Prance 1989) and diverse terrestrial ecosystem on earth (containing more than 10% of its species: Pires & Prance 1985). Not surprisingly the rainforest influences the entire world's weather patterns and climate (Keller *et al.* 2004).

The majority of the Amazonian rainforest is unflooded (generally referred to as *terra firme* forest-type), located in areas lower than 100 m elevation and sharing much structural similarity with unflooded rainforests throughout the rest of the Neotropics (Kalliola *et al.* 1991, Worbes *et al.* 1992, Everham *et al.* 1996, Pitman *et al.* 2001, Tuomisto *et al.* 2003). The low relief of the Amazon basin, however, leads to extensive flooding which varies in frequency, duration, depth and local spatial variation (Myster 2009), explaining much of the tree distribution, composition, abundance, and association (Junk 1989). Most of the flooded water is nutrient rich “white” water from the Andes, which creates the forest-type generally called várzea, and the rest is "black/clear" water which is nutrient poor forest runoff and creates the forest-type generally called igapó *(Junk 1989)*. The resulting flooded forests cover at least 120,000 square km across the landscape of the Amazon basin (Parolin *et al.* 2004) and have been shown to have a unique biology and ecology (Kalliola *et al.* 1991). This flooding dynamic then, along with differences in, at least, biota and soil characteristics (Junk 1989, Honorio 2006), creates complex and diverse forest associations throughout the Amazon basin (Myster 2009).

Therefore in order to better understand how these Amazonian rainforests are structured, and to collect data urgently needed in the Neotropics for their sound, sustainable management, I expand on past sampling of Amazon forests (Valcenia *et al.* 2004a, Valencia *et al.* 2004b, Valencia *et al.* 2004c, Myster 2007, Myster 2010, Myster 2015a, Myster 2015b, Myster 2015c,) by setting up and sampling four 2500 m^2 plots of the igapó forest-type and four 2500 m^2 plots of the várzea forest-type. The aim of the research is to use that data to compile floristics and to compute these forest structural parameters – tree stem size variation, mean, maximum and total, dispersion pattern and degree of clumping, canopy closure, basal area, above-ground biomass – in both forests, and then test these hypotheses:

Hypothesis I: Igapó forest will have less families, less genera and less species than a várzea forest with the same flooding duration, with few species in common (Junk *et al.* 2010).

Hypothesis II: Igapó forest will have less tree stems, especially small stems, compared to a várzea forest with the same flooding duration (Junk *et al.* 2010).

MATERIALS AND METHODS

The first study site is the Area de Conservation Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: Myster 2007, Myster 2009, Myster 2010) located in Loreto Province, 80 miles southeast of Iquitos, Peru (~2° S, 75° W) with an elevation of ~100 m asl. The reserve is part of one of the largest protected areas in the Amazon, containing wet lowland tropical rainforest (Holdridge 1967) of high diversity (Daly & Prance 1989, Daly *et al.* 2000). It is comprised of low, seasonally inundated river basins of the upper Amazon and named for two of the major white-water rivers (the Tahuayo and the Tamshiyacu) which form boundaries to the north and west, creating large fringing floodplains (Junk 1989). The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation ranges from 2.4 – 3.0 m per year, and the average temperature is relatively steady at 26°C. Within the ACRCTT are areas of black/clear water runoff which create igapó forests of differing frequency, duration, and maximum water column height, where the rainy season is between November and April (Kalliola *et al.* 1991). Common tree species include *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata*, *Phytelephas macrocarpa*, *Guazuma rosea*, and *Piptadenia pteroclada* (Daly & Prance 1989, Myster 2007, Prance 1979, Puhakka *et al.* 1992).

The second study site is the Yasuni Research Station (YRS: 0°41' S, 76°24' W), operated by the Pontificia Universidad Catolica of Ecuador and located within the Yasuni National park of eastern Ecuador (Svenning 1999, Duivenvoorder 2001, Myster & Santacruz 2005, Metz *et al.* 2008, Myster 2012a, Myster 2014, Myster 2015a). Most of the YRS is *terra firme* forest which has been classified as lowland tropical rainforest (Holdridge 1967).

The mean annual rainfall is 3 m with the wettest months April to May and October to November. August is the driest month and the mean monthly temperature varies between 22°C and 35°C. Soils in the National park have been described as clayey, low in most cations but rich in aluminum and iron, whereas soils at the station in *terra firme* forest are acidic and rich in exchangeable bases with a texture dominated by silt (Tuomisto *et al.* 2003). The park has low topographic variation with a mean elevation of approximately 200 m above sea level. The station is the site of a long-term 50 ha vegetation plot in *terra firme* forest, maintained by the Smithsonian Tropical Research Institute (Losos and Leigh 2004), parts of which have been sampled (Valencia *et al.* 2004a, Valencia *et al.* 2004b, Valencia *et al.* 2004c, Valencia *et al.* 2009). Also found at YRS is várzea floodplain forest - located next to the nutrient rich whitewater Tiputini River - which is inundated a few weeks between the months of October and April to a maximum depth of 3 m.

In May 2011 at the ACRCTT, my field assistants and I set up four 50 m x 50 m plots randomly placed within the igapó forest-type which is under black-water 1-2 months every year. We then tagged and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in each plot (Myster 2013). The dbh measurement was taken at the nearest lower point where the stem was cylindrical and for buttressed trees it was taken above the buttresses. In June 2013, the tagged trees were identified to species, or to genus in a few cases, using Romoleroux *et al.* (1997) and Gentry (1993) as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana herbarium and the web site of the Missouri Botanical Garden.

In May 2010 at YRS, my field assistants and I set up four 50 m x 50 m plots randomly placed within the várzea forest-type which is under white-water 1-2 months every year. These plots were located close to the Tiputini river and only a few hundred meters from the 50 ha *terra firme* plot (Losos & Leigh 2004). We then tagged, identified, and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in all plots (Myster 2013). The trees were identified using the same protocol as the plot at ACRCTT. The data for all plots is archived at the Luquillo Experimental Forest as LTERDBAS#172 as part of the LTER program funded by the US National Science Foundation.

From the data in each of the eight 2500 m^2 plots, I first compiled floristic tables of family, genus and species and then generated (1) the total number of stems, the mean and maximum among those stems, and the number of stems in each of four size classes: 10 < 20 dbh, 20 < 30 dbh, 30 < 40 dbh and ⩾ 40 dbh, (2) the stem dispersion pattern (random, uniform, clumped) computed by comparing plot data to Poisson and negative binomial distributions using Chi-square analysis and, if clumped, greens index was also computed to access degree of clumping (Ludwig & Reynolds 1988, Myster & Pickett 1992), (3) canopy closure using the formula in Buchholz *et al.* (2004) for tropical trees with the resulting percentage of the 1 ha plot area closed, (4) total basal area as the sum of the basal areas of all individual stems (Πr^2; where r = the dbh of the individual stem / 2) and (5) above-ground biomass (AGB) using the formula in Nascimento & Laurance (2001) suggested for tropical trees of these stem sizes.

RESULTS AND DISCUSSION

The four 50 m x 50 m igapó plots showed substantial variation in floristics and (when combined) had 16 families, 29 genera and 31 species (Table 1). Fabaceae was the most abundant family which also had the most genera and the most species. The family

Arecaceae was also abundant and Meliaceae was the only family with only one stem. Genera with more than one species were *Astrocaryum, Tovomita, Parkia, Eschweilera and Mouriri*. The most abundant species were *Aldina latifolia* with nine stems and *Caraipa grandifolia*, *Mabea* sp., *Hydrochori* sp., *Virola elongate* and *Psychotria lupulina* with eight stems (Table 1).

The four 50 m x 50 m várzea plots also showed substantial variation in floristics and (when combined) had 42 families, 91 genera and 159 species (Table 2). Fabaceae was the most abundant family which also had the most genera and the most species. The families Melastomataceae and Moraceae were also abundant and many families had only one stem. Genera with more than one species were *Inga, Duguetia, Xylopia, Aspidosperma, Ceiba, Matisia, Protium, Cecropia, Liconia, Vismia, Alchornea, Macrolobium, Casearia, Nectandra, Eschweilera, Gustavia, Mouriri, Miconia, Guarea, Brosimum, Sovocca, Ficus, Virola, Coussarea, Cupania, Talisia, Pouteria* and *Leonia*. The most abundant species were all in Fabaceae: *Inga spectabilis* (24 stems), *Macrolobium acasifolium* (19), *Inga leiocalycina* (13), *Inga alata* (12), *Inga cinnamomea* (7) and *Inga nobilis* (9) (Table 2). There were only four species in common between the two forest-types: *Euterpe precatoria*, *Guarea macrophylla*, *Brosimum lactescens* and *Qualea paraensis*.

In terms of physical structure, there was much agreement among the 2500 m^2 plots within each forest-type (Table 3). In general, flooding reduced the number of stems and the average stem size in both composite plots compared to unflooded *terra firme* forest (Table 4). Whereas igapó basal area was low, várzea basal area was in the middle of the range sampled in the three *terra firme* plots, one of which was located close to the várzea study plot (see papers by Valencia *et al.* 2004a,b,c). Above-ground biomass was larger in *terra firme* compared to either flooded forest. Both composite study plots conformed to the reverse J stem size distribution pattern for all stems with a smaller proportion in the largest stem size class than the várzea study plot (Table 4). The igapó forest did, however, have the largest individual tree of 91 cm dbh, as well as a smaller average tree stem diameter.

The structural parameters for palm forest and white sand forest show forests of even greater reduction in structure compared to both of the flooded forests (Table 5). The várzea composite plot had more stems than either of the unflooded palm forest or white sand forest plots, which had more than the igapó plot (Table 5). These trends (várzea > palm > white sand > igapó) held true for the smaller stem sizes but white sand forest had the most stems between 20 and 29 cm dbh and between 30 and 30 cm dbh, with the várzea plot having the most stems at least 40 cm dbh. For species, basal area and above-ground biomass, várzea was again the most but with a trend (várzea > white sand > palm > igapó) change. Canopy closure went back to the previous trend.

Both hypotheses I and II were generally accepted. While the igapó plot had less families, genera and species compared to the várzea plot, Fabaceae was the most common family in both plots. There was little similarity in genera and species. Igapó also had less structure in total stems, size of stems, basal area and above-ground biomass. These differences may have been the result of the poorer nutritive quality of black-water compared to white-water. *Terra firme* plots in the Peruvian Amazon had more stems, larger stems and more basal area and above-ground biomass than both of these flooded plots (author, unpubl. sampling). Also the degree of flooding in the two study plots was not enough to mimic structural losses seen in two unflooded forests with low soil nutrients (palm and white sand plots also in Peru:author, unpubl. sampling) because the várzea was generally more and the igapó plot was generally less than palm and white sand forests.

For these study plots the flooding may have been so serve that there was few "threshold" sizes that stems could obtain to escape the flooding, and so the reduction in stems number with increasing stem size (reverse J) was maintained. While the average stem size was similar between the two study flooded forests and a *terra firme* sampling, more stems were lost as flooding duration increased with proportionally more medium-sized stems gained. The amount of flooding in várzea was not enough to reduce basal area, but it was enough in igapó. Basal area shows the influence of the large individuals because a decrease in stem numbers is offset with larger stems.

The study composite plot in várzea forest compared well to other várzea samplings in all regards except for low ABG (Wittmann *et al.* 2002,Wittmann & Junk 2003). This study composite plot had more large stems than the reverse J distribution found in the 50 ha plot (Valencia *et al.* 2004a) and in *terra firme* forests within the Yasuni National Park (Pitman *et al.* 2002) and at other Amazon sites (Korning *et al.* 1990). This suggests that while smaller stems die from flooding, a stem may survive to a large size if it can reach a certain size and take advantage of the resources that the dead stems are not now using. Consequently, the study composite plot in várzea forest had a large basal area for stems at least 40 cm in diameter in base diameter. The canopy opened up with the stem loss but the low amount of clumping suggests the dominance of flooding, over other factors such as biological interactions, in determining stem survival and growth. I also found in these plots (Myster 2015a) that the seven most common families were also among the top ten families found in multiple samplings in the nearby 50 ha plot (Valencia *et al.* 2004a, Valencia *et al.* 2004b, Valencia *et al.* 2004c) but at the genus and species taxonomic level, similarities with the 50 ha plot samplings disappear except for the genera *Cecropia, Lachornea, Inga, Zygia, Eschweilera and Virola* and the species *Iriartea deltoidea* and *Coccoloba densifrons*. Also because the várzea forest loses families, genera and species proportionally more than it loses stems compared to *terra firme* forest, fisher's α was lower (Myster 2015a).

I also found in ACRCTT forests that differed in flooding duration (unflooded [dry], flooded by black water 1-5 months per year [wet], flooded by black water 6 months per year [very wet]: (Myster 2007, Myster 2010, Myster 2015c) tree stems and canopy coverage declined as flooding increased, more so than reductions due to treefall, trees were clumped only in the gaps for wet forest, and there were smaller stems in gaps compared to all adjacent forests. Consequently flooding was a greater stressor on these forests than treefall where Amazonian forests may have gradients (flooding) and disturbances (treefall) which overlap in their traditional roles, presenting plants with similar cues. Common species existed between wet forests and their gaps and between wet and very wet gaps, and tree richness was maximum in dry forest and minimum in very wet gaps. Finally there was a significant effect of degree of treefall gap formation on canopy average height, canopy maximum height, basal area, density, above-ground biomass, turnover, and alpha diversity, and a significant effect of flooding on species richness, genera richness, density, turnover, and alpha diversity. Moreover there were fewer but larger trees, and more production in the forest plots compared with the gap plots; and the very wet plots had fewer trees, species, and genera compared with the other forests. The greatest amount of turnover was also found in the very wet forest with the wet forest had the greatest richness and alpha diversity. Results supported a "mass effects" hypothesis where species from both the unflooded and most flooded forests and their gaps have overlapping ranges in the less flooded forest and gaps, causing continuous immigration which boosts diversity (Myster 2007, Myster 2010, Myster 2015c).

All four samplings of the 50 ha plot at YRS had more stems than either of the study plots, also true in the 15 other unflooded forests (all stems at least 10 cm dbh) sampled in Yasuni National Park (Pitman *et al.* 2002). Total basal area, however, is comparable among the flooded forests and the 50 ha plot, because the flooded forests make up in size what it losses in stem numbers. The density of tree stems and their size distributions in the study plots compared well with other Western Amazon flooded forests as well (Myster 2009, Ferreria 1997, Pitman *et al.* 1999). Several structural parameters conformed to the flooding gradient, decreasing in complexity as flooding increased, which may be due in part to root burial by sedimentation and oxygen deficiency in flooded forests (Junk 1989). The loss of tree stem density with flooding (Balslev *et al.* 1987) may be explained by the loss of tree stems due to the action of moving water or the physical damage due to the weight of debris (falling branches as reviewed in Myster 1993). Clumping was less than that found in larger forest openings recovering from agriculture (Myster & Pickett 1992) which may have contained more perching opportunities or bird to land and disperse seeds.

In terms of forest structure, these forests do lose stems from flooding but that loss is not proportionally similar across all size classes. Flooded forests maintain a greater number of larger trees than unflooded forests and so their stem distribution is more of a "saddle" than a monotonic decline in numbers with increasing size, as seen in the basal area, leading to fewer trees, genera, and species as flooding increased (Myster 2010). Indeed flooding tends to eliminate both vertical and horizontal heterogeneity affecting, for example, the availability of commonly logged tree species and animal populations. It must be remembered, however, that those studies and this one were only "snapshots" of forest structure and that in order to completely understand forest structure, longer term sampling with larger plots is needed across the Amazon landscape. Such studies will show that the underlying process of these forests, as for all plant communities, is plant-plant replacement (Myster 2012b). These permanent plot studies, and others like them at different points on the Amazonia landscape, provide baseline data on forest dynamics and fluctuations of forest structure. This knowledge will enable conservationists to develop sound management techniques for these forests in order to better utilize them as societal and human needs arise in the future. Sustainability of these flooded systems in the Amazon is critical for the lives of the local peoples that live there but also for the rest of us.

The most obvious conclusion of these two samplings, and others done in the same forest types across the Amazon basin landscape, is that flooding reduces forest structure. This can be seen in total stem density, basal area and ABG when comparing the study plots with *terra firme* plots. Flooding can, however, merely change structure, as seen in stem size distribution pattern. Such results from the study plots beg the question: What aspects of the flooding regime (Myster 2009) are most important and for what aspects of structure? To date researchers have pointed to differences in water nutritional quality vs. flooding duration with its correlated maximum water height. With the only two samplings done here, it is difficult to tease apart these differences. The comparison with other forests of the same water type helps to a degree but much more sampling and computation in the Amazon is needed. There may be other ways to look at flooding which warrant further study, such as the effects of flooding frequency and sedimentation. Only then may we be able to

Table 1. All stems sampled in the four igapó plots sorted by family, then by genus and finally by species. Number of stems in each plot is given.

family	genus	species	#plot1	#plot2	#plot3	#plot4
Apocynaceae	*Microplum*	*anomala*	0	1	2	0
Arecaceae	*Astrocaryum*	*jauari*	2	1	2	2
Arecaceae	*Astrocaryum*	*murumura*	1	0	0	0
Arecaceae	*Euterpe*	*precatoria*	0	0	2	3
Arecaceae	*Oenocarpus*	*mapora*	0	1	1	0
Arecaceae	*Socratea*	*exorrhiza*	0	2	1	0
Calophyllaceae	*Caraipa*	*grandifolia*	3	2	1	2
Chrysobalanaceae	*Hirtella*	*racemosa*	0	0	1	0
Chrysobalanaceae	*Licania*	sp.	0	2	0	2
Clusiaceae	*Tovomita*	*macrophylla*	1	0	0	2
Clusiaceae	*Tovomita*	sp.	1	1	1	1
Euphorbiaceae	*Mabea*	sp.	1	3	1	3
Fabaceae	*Aldina*	*latifolia*	3	3	2	1
Fabaceae	*Campsiandra*	*augustifolia*	0	0	1	4
Fabaceae	*Crudia*	*amazonica*	2	0	0	0
Fabaceae	*Cynometra*	*spruceana*	0	0	1	0
Fabaceae	*Hydrochori*	sp.	1	1	3	3
Fabaceae	*Macrosamanea*	*amplissima*	1	2	0	2
Fabaceae	*Parkia*	*auriculata*	0	0	1	0
Fabaceae	*Parkia*	*pectinata*	2	0	2	2
Fabaceae	*Pithecellobium*	sp.	0	0	0	2
Lauraceae	*Nectandra*	sp.	0	1	0	0
Lauraceae	*Ocotea*	*aiiphylla*	0	0	3	1
Lecythidaceae	*Eschweilera*	*albiflora*	2	2	2	0
Lecythidaceae	*Eschweilera*	*parriflora*	1	2	0	4
Malpighiaceae	*Acmanther*	*latifolia*	3	1	0	0
Malvaceae	*Theobroma*	*cacao*	2	0	2	0
Melastomataceae	*Mouriri*	*apiranga*	1	1	0	0
Melastomataceae	*Mouriri*	*grandiflora*	0	1	0	0
Melastomataceae	*Mouriri*	*myrtifolia*	0	2	1	3
Meliaceae	*Guarea*	*macrophylla*	0	1	0	0
Moraceae	*Brosimum*	*lactescens*	2	0	2	1
Moraceae	*Maquira*	*coriacea*	1	1	2	1
Moraceae	*Trymatoco*	*amazonicus*	0	0	0	1
Myristicaceae	*Virola*	*elongate*	3	3	0	2
Rubiaceae	*Ferdinandu*	*rudgeoides*	0	0	4	0
Rubiaceae	*Psychotria*	*lupulina*	2	2	3	1
Salicaceae	*Casearia*	sp.	0	2	0	0
Sapotaceae	*Manikara*	*bidentata*	1	1	0	0
Sapotaceae	*Pouteria*	*elegans*	2	0	0	1
Vochysiaceae	*Qualea*	*paraensis*	0	2	2	1

Table 2. All stems sampled in the four várzea plots sorted by family, then by genus and finally by species. Number of stems in each plot is given.

family	genus	species	#plot1	#plot2	#plot3	#plot4
Anacardiaceae	*Tapirira*	*guianensis*	1	0	0	0
Annonaceae	*Xylopia*	*ligustrifolia*	2	1	0	0
Annonaceae	*Duguetia*	*quitarensis*	0	0	1	0
Annonaceae	*Duguetia*	*spixiana*	1	1	0	0
Annonaceae	*Oxandra*	*mediocris*	0	0	0	1
Annonaceae	*Xylopia*	*ligustrifolia*	2	0	1	0
Annonaceae	*Xylopia*	*ligustrifolia*	1	1	1	0
Apocynaceae	*Aspidosperma*	*darianense*	0	1	0	0
Apocynaceae	*Aspidosperma*	*rigidum*	0	0	0	1
Aposinaceae	*Lacmellia*	*lactescens*	0	1	0	0
Arecaceae	*Astrocaryum*	*chambira*	1	0	0	0
Arecaceae	*Wettinia*	*mainensi*	0	0	1	0
Arecaceae	*Triartea*	*deltoidea*	2	0	1	0
Arecaceae	*Euterpe*	*precatoria*	0	0	0	1
Arecaceae	*Oenocarpus*	*batagua*	0	0	1	0
Bignoniaceae	*Jacaranda*	*copaia*	0	0	0	1
Bixaceae	*Bixa*	*urucurama*	0	1	0	0
Bombacaceae	*Ceiba*	*samauma*	1	0	0	0
Bombacaceae	*Ceiba*	*pentandra*	1	0	0	0
Bombacaceae	*Matisia*	*bracteolosa*	0	0	1	0
Bombacaceae	*Matisia*	*malacocalix*	1	1	0	0
Bombacaceae	*Pachira*	*schunkey*	0	1	0	0
Bombacaceae	*Quararibea*	*wittii*	0	0	1	0
Burseraceae	*Crepidosperum*	*rhoifolium*	0	1	0	0
Burseraceae	*Protium*	*amazonicum*	0	1	0	0
Burseraceae	*Protium*	*grannodu*	1	0	0	0
Burseraceae	*Protium*	*sagatianum*	0	1	0	0
Burseraceae	*Tetragastris*	*panamensis*	0	0	1	0
Burseraceae	*Trattinickia*	*glasiavii*	0	0	0	1
Cecropiaceae	*Cecropia*	*latiloba*	2	0	0	0
Cecropiaceae	*Cecropia*	*membrancea*	0	0	3	0
Cecropiaceae	*Coussapoa*	*orthoneura*	1	1	0	0
Chrysobalanaceae	*Hirtella*	*excelsa*	0	0	0	1
Chrysobalanaceae	*Licania*	*urceolaris*	0	0	1	0
Chrysobalanaceae	*Licania*	*zigzag*	1	0	0	0
Chrysobalanaceae	*Licania*	*nervifina*	0	0	1	0
Chrysobalanaceae	*Licania*	*glablanca*	0	0	1	0
Clusiaceae	*Caraipa*	*myricoides aff.*	0	0	0	1
Clusiaceae	*Vismia*	*baccifera*	0	1	0	0
Clusiaceae	*Vismia*	*macrophylla*	1	0	0	0
Clusiaceae	*Vismia*	*myrtoide*	0	0	1	0
Combretaceae	*Buchenavia*	*machrophylla*	0	1	0	0
Dicapetalaceae	*Tapura*	*juruana*	1	0	0	0
Ebenaceae	*Diospyros*	*hipofuzzy*	1	0	0	0
Elaeocarpaceae	*Sloanea*	*guianensis*	1	0	0	0
Elaeocarpaceae	*Sloanea*	*pequrba*	0	0	0	1

Continue Table 1

family	genus	species	#plot1	#plot2	#plot3	#plot4
Euphorbiaceae	*Alchornea*	*schumburkii*	0	1	0	0
Euphorbiaceae	*Alchornea*	*latifolia*	1	1	0	0
Euphorbiaceae	*Alchornea*	*triplinervia*	0	1	0	0
Euphorbiaceae	*Alchorneopsis*	*floribunda*	0	0	1	0
Euphorbiaceae	*Mabea*	*superbrandu*	0	1	0	0
Euphorbiaceae	*Sagotia*	*racemosa*	1	1	0	0
Fabaceae	*Brownea*	*lore*	0	0	2	0
Fabaceae	*Brownea*	*grandiseps*	0	0	0	1
Fabaceae	*Dialium*	*guianense*	0	0	0	2
Fabaceae	*Inga*	*alangosta*	0	1	1	0
Fabaceae	*Inga*	*alata*	5	2	3	2
Fabaceae	*Inga*	*acreana*	1	0	0	0
Fabaceae	*Inga*	*bourgoni*	1	1	1	0
Fabaceae	*Inga*	*cinnamomea*	2	2	2	1
Fabaceae	*Inga*	*leiocalycina*	3	3	7	0
Fabaceae	*Inga*	*marginata*	0	0	1	0
Fabaceae	*Inga*	*nobilis*	1	2	4	2
Fabaceae	*Inga*	*punctata*	0	0	0	1
Fabaceae	*Inga*	*sarayacoensis*	0	1	0	0
Fabaceae	*Inga*	*sertulifera*	0	0	0	1
Fabaceae	*Inga*	*spectabilis*	10	5	5	4
Fabaceae	*Inga*	*umbratica*	1	0	1	0
Fabaceae	*Macrolobium*	*acasifolium*	3	5	5	6
Fabaceae	*Macrolobium*	*Yasuni*	0	0	1	0
Fabaceae	*Ormosia*	*paraensis*	0	0	0	1
Fabaceae	*Parkia*	*velutina*	1	0	0	0
Fabaceae	*Pterocarpus*	*asimile*	0	0	1	0
Fabaceae	*Swartzia*	*multijuga*	0	1	0	0
Fabaceae	*Zigia*	*grandiflora*	1	1	1	2
Flacourtiaceae	*Alchornea*	*latifolia*	0	1	0	0
Flacourtiaceae	*Casearia*	*aculeate*	0	0	1	0
Flacourtiaceae	*Casearia*	*arborea*	0	0	0	1
Flacourtiaceae	*Casearia*	*bracteifera*	1	0	0	0
Flacourtiaceae	*Laetia*	*procera*	1	1	0	0
Lauraceae	*Aniba*	*hostmanniana*	0	0	0	1
Lauraceae	*Aniba*	*panurensis*	1	0	0	0
Lauraceae	*Dacytyla*	*rower*	0	0	1	0
Lauraceae	*Nectandra*	*graninpreso*	1	0	0	0
Lauraceae	*Nectandra*	*yarienensis*	0	1	0	0
Lauraceae	*Ocotea*	*javitensi*	1	0	0	0
Lecythidaceae	*Couratari*	*guianensis*	1	0	0	0
Lecythidaceae	*Eschweilera*	*bracteosa*	0	0	0	1
Lecythidaceae	*Eschweilera*	*coriacea*	0	0	1	1
Lecythidaceae	*Eschweilera*	*tessmanii*	1	0	0	0
Lecythidaceae	*Gustavia*	*hexapetala*	0	0	2	0
Lecythidaceae	*Gustavia*	*longifolia*	1	0	0	1
Melastomataceae	*Mouriri*	*rugosa*	0	0	1	0
Melastomataceae	*Mouriri*	*grandiflora*	0	0	1	0
Melastomataceae	*Miconia*	*sachapurp*	0	0	0	1

Continue Table 1

family	genus	species	#plot1	#plot2	#plot3	#plot4
Melastomataceae	*Miconia*	*pilgeriana*	0	1	0	0
Melastomataceae	*Bellusia*	*pentamera*	1	0	0	0
Melastomataceae	*Miconia*	*tipica*	0	1	0	0
Melastomataceae	*Miconia*	*leandrablanca*	0	1	0	0
Melastomataceae	*Miconia*	*poeppigii*	1	0	0	0
Meliaceae	*Guarea*	*macrophylla*	1	0	0	0
Meliaceae	*Guarea*	*silvatica*	0	0	1	0
Meliaceae	*Trichilia*	*pallida*	0	0	1	0
Meliaceae	*Guarea*	*purusana*	0	0	0	1
Meliaceae	*Guarea*	*guentheri*	0	0	0	1
Mirtaceae	*Eugenia*	*smedcomun*	1	0	0	0
Moraceae	*Sorocea*	*steinbachii*	0	1	0	0
Moraceae	*Brosimum*	*lactescens*	0	0	1	0
Moraceae	*Ficus*	*perisiana*	0	0	1	0
Moraceae	*Brosimum*	*guianense*	1	0	0	0
Moraceae	*Maquira*	*quianensis*	1	0	0	0
Moraceae	*Pseudolmedia*	*laevis*	1	0	0	0
Moraceae	*Perebea*	*mollis*	0	0	0	1
Moraceae	*Sorocea*	*oligotricha*	0	1	0	0
Moraceae	*Ficus*	*guianensis*	0	1	0	0
Myristicaceae	*Virola*	*x*	0	0	1	0
Myristicaceae	*Virola*	*surinamensi*	0	0	2	1
Myristicaceae	*Virola*	*ovobata*	1	0	0	0
Myristicaceae	*Virola*	*peruviana*	0	0	1	0
Nyctaginaceae	*Neea*	*pantano*	0	0	0	1
Ochnaceae	*Ouratea*	*superba*	0	0	1	0
Olacaceae	*Minquartia*	*guianensis*	1	0	0	0
Opiliaceae	*Agonandra*	*silvatica*	0	1	0	0
Pichramnaceae	*Picrannia*	*micro*	0	0	1	0
Pichramnaceae	*Picrannia*	*mini*	0	0	0	1
Polygonaceae	*Coccoloba*	*densifrons*	0	1	0	0
Polygonaceae	*Triplaris*	*wilgeltiana*	1	0	0	0
Rubiaceae	*Faramea*	*capillipes*	1	0	0	0
Rubiaceae	*Warszewiczia*	*coccinea*	0	0	1	0
Rubiaceae	*Alibertia*	*jorge*	0	1	0	0
Rubiaceae	*Pentagonia*	*paviflora*	1	0	0	0
Rubiaceae	*Coussarea*	*retidomati*	0	0	0	1
Rubiaceae	*Coussarea*	*membradomat*	0	1	0	0
Rubiaceae	*Psychotria*	*membradomat*	0	0	1	0
Sabiaceae	*Meliosma*	*doly*	0	1	0	0
Sabiaceae	*Ophyocarium*	*heterophyllum*	0	1	0	0
Sapindaceae	*Cupania*	*cinerea*	0	0	0	1
Sapindaceae	*Cupania*	*scrobiculata*	0	0	0	1
Sapindaceae	*Talisia*	*ndovogranatensis*	0	0	1	0
Sapindaceae	*Talisia*	*pulvinote*	0	1	0	0
Sapotaceae	*Pouteria*	*durlandii*	0	1	0	0
Sapotaceae	*Pradosia*	*atroviolata*	0	0	0	2
Sapotaceae	*Chrysophylum*	*venezuelanense*	1	0	0	0
Sapotaceae	*Pouteria*	*guianensi*	0	0	1	0
Sapotaceae	*Pouteria*	*doradagrande*	1	0	0	0

Continue Table 1

family	genus	species	#plot1	#plot2	#plot3	#plot4
Sapotaceae	*Pouteria*	*angostalooppii*	0	0	0	1
Simarubiaceae	*Simaruba*	*amara*	0	0	1	0
Simarubiaceae	*Simaba*	*parraensis*	0	1	0	0
Sterculiaceae	*Sterculia*	*fronddosa*	0	0	0	1
Sterculiaceae	*Theobroma*	*subincanum*	1	0	0	0
Tiliaceae	*Apeiba*	*membranacea*	0	0	1	0
Tiliaceae	*Mollia*	*gracilis*	1	0	0	0
Ulmaceae	*Ampelocera*	*edentula*	1	0	0	0
Violaceae	*Leonia*	*crasa*	0	0	0	1
Violaceae	*Leonia*	*glycicarpa*	0	0	0	1
Vochysiaceae	*Qualea*	*paraensis*	0	1	0	0
Vochysiaceae	*Vochysia*	*braceliniac*	1	0	0	0

discover the causes of Amazon flooded forest structure.

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Table 3. Physical structure parameters for all trees at least 10 cm dbh sampled in the four igapó plots (i1,i2,i3,i4) and the four várzea plots (v1,v2,v3,v4).

Parameter	i1	i2	i3	i4	v1	v2	v3	v4
Stem density :								
Total	41	42	44	40	120	125	115	113
10 < 19 dbh	23	19	21	21	91	94	88	93
20 < 29 dbh	15	13	17	13	22	20	24	21
30 < 39 dbh	4	6	2	5	11	9	8	11
40 or greater	2	2	3	1	20	20	20	21
mean	22.6	23.0	21.4	22.2	24.5	22.9	25.4	24.0
Species richness	22	25	24	23	57	49	50	39
Basal area (m^2)	1.52	1.63	1.57	1.70	6.25	7.10	6.55	6.45
Above-ground biomass (Mg)	52	49	51	50	84	86	80	82
Canopy:								
Closure (m^2)	1134	1228	1329	1233	4488	4558	4368	4498
per plot (%)	11.34	12.28	13.29	12.33	44.88	45.58	43.68	44.98
Dispersion:								
spatial pattern	clumped	clum.	Clum.	Clum.	Clum.	Clum.	Clum.	Clum.
green's index	0.18	0.12	0.16	0.15	0.03	0.04	0.00	0.01

Table 4. Physical structure parameters for all trees at least 10 cm dbh sampled in the four igapó plots combined into a 1 ha plot for comparative purposes and physical structure parameters for all trees at least 10 cm dbh sampled in the four várzea plots combined into a 1 ha plot for comparative purposes. They are then compared to three 1 ha samplings in Amazonian *terra firme* forest.

Parameter	igapó plot	várzea plot	*terra firme* plot[1]	*terra firme* plot[2]	*terra firme* plot[3]
Stem density :					
Total	167	573	604 – 725	605.3	734
10 < 19 dbh	84	366	--	--	--
20 < 29 dbh	58	87	--	--	--
30 < 39 dbh	17	39	--	--	--
40 or greater	8	81	--	--	--
mean	22.3	24.2	--	21.7	--
Species richness	31	159	--	--	--
Basal area (m^2)	6.52	26.35	22.2 – 31.2	32.6	22.2
Above-ground biomass (Mg)	202	292	--	457.8	--
Canopy:					
Closure (m^2)	1231.22	4478.04	--	--	--
per ha (%)	12.3122	44.7804	--	--	--
Dispersion:					
spatial pattern	clumped	clumped	--	--	--
green's index	0.17	0.02	--	--	--

[1]Valencia *et al.* (2004abc), [2]Haugaasen & Peres (2006), [3] Korning *et al.* 1990.

Table 5. Physical structure parameters for all trees at least 10 cm dbh sampled in four igapó plots combined into a 1 ha plot for comparative purposes and physical structure parameters for all trees at least 10 cm dbh sampled in four várzea plots combined into a 1 ha plot for comparative purposes. They are then compared to a 1 ha sampling in Amazonian palm forest in the Peruivan Amazon (author, unpubl. data) and to a 1 ha sampling in Amazonian white sand forest in the Peruivan Amazon (author, unpubl.data).

Parameter	igapó plot	várzea plot	palm plot	white sand plot
Stem density :				
Total	167	573	449	403
10 < 19 dbh	84	366	341	241
20 < 29 dbh	58	87	77	95
30 < 39 dbh	17	39	24	63
40 or greater	8	81	6	3
mean	22.3	24.2	14.1	19.8
Species richness	31	159	57	103
Basal area (m^2)	6.52	26.35	11.5	12.52
Above-ground biomass (Mg)	202	292	267.3	386.7
Canopy:				
Closure (m^2)	1231.22	4478.04	2356.7	1441.2
per ha (%)	12.3122	44.7804	23.567	14.412
Dispersion:				
spatial pattern	clumped	clumped	random	random
green's index	0.17	0.02	--	--

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