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The Effects of Flooding on Forest Floristics and Physical Structure in the Amazon: Results from Two Permanent Plots

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Abstract

I investigated how flooding affects floristics and physical structure of forests in the Amazon at the Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo, Loreto ProvinceIquitos, Peru and at the Yasuni Experimental Station, Yasuni National Park, Ecuador. Iset up and sampled 1 ha permanent plots next to a black-water river (igapó forest) in Peru and next to a white-water river (várzea forest) in Ecuador. I found (1)16 families in the 1 haigapó plot with Fabaceae the most common family, (2) várzeastems conformed to a reverse J size pattern for stems less than 40 cm dbh but had more large stems, total stems were within other várzea forest ranges with a slightly larger average dbh, trees were clumped at a low level with 45% canopy closure and while the basal area was also within other várzeaforest ranges, above-ground biomass was lower, (3) igapóstems conformed to the reverse J size pattern, total stems were lower than other igapóforest ranges with a slightly larger average dbh, trees were clumped at a higher degree than the várzea forest with 12% canopy closure while the basal area and above-ground biomass was less than both other igapó samplings and the várzea study plot, and (4) flooding produced reduced basal area in igapó, and smaller stems, stem densities and above-ground biomass for both flooded forests. I conclude that both study plots show a reduction of tree stem density and structure (basal area, above-ground biomass) with flooding, which reduces even more as months under water increase. More sampling in these forests is needed, however, before a conclusion about which aspect of the flooding regime –e.g., water quality, flooding duration or frequency – is most important in determining different aspects of forest structure. Permanent plot studies in the Amazon, like this one, provide much needed data for intelligent management decisions and the development of sustainability techniques.

Keywords: igapó; Tamshiyacu-Tahuayo;T ipitini; várzea; Yasuni

Introduction

The Amazon is the mightiest river in the world, having a discharge of fresh water 4–5 times greater than that of the next mightiest river, the Congo. The Amazon is also the second longest river in the world, originating in the foothills of the Andean Mountains of South America and running 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 a.s.l. Associated with this watershed is the largest continuous rainforest in the world, located in the equatorial regions of Brazil, Columbia, Ecuador, Bolivia and Peru. Besides the Andes and the Atlantic Ocean, the watershed is bounded to the north by the Guiana crystalline shield and to the south by the Brazilian crystalline shield [1] marked at their edges by cataracts in the rivers.

The Amazonian rainforest encompasses over 6,000,000 square kilometers [2] and is the most productive [3] and diverse terrestrial ecosystem on earth (containing more than 10% of its species) [1]. Not surprisingly this rainforest influences the entire world’s weather patterns and climate [4] and may even control how much rainfall it itself receives [1]. Perhaps most importantly for the human future the Amazonian rainforest interacts intimately with the Earths carbon (C) cycle acting both as a carbon “sink”, by taking in large amounts of CO_2 through photosynthesis, but also as a carbon “source” as, for example, when its plants decay or burn. Critically, this rainforest will continue in the future to both contribute to, and suffer from, the effects of global warming.

The majority of the Amazonian rainforest is unflooded (generally referred to as *terra firme*), located in areas lower than 100 m elevation and sharing much structural similarity with unflooded rainforests throughout the rest of the Neotropics [5-7]. Within that broad classification are types of *terra firme* which differ largely in soil characteristics (e.g., *terra firme* proper on clay or loam soils, white sand forests on soils with large amounts of quartz, palm or swamp forests often on standing water) [8].

The low relief of the Amazon basin leads to extensive flooding which varies in frequency, duration, depth and local spatial variation [9], explaining much of the tree distribution, composition, abundance, and association [10]. Most of the flooded water is nutrient rich “white” water from the Andes, which creates forests generally called várzea, and the rest is “black/clear” water which is nutrient poor forest runoff and creates forests generally called igapó [10] or a mixture of the two [9]. The resulting flooded forests cover at least 120,000 square kilometers [11] and have been shown to have a unique biology and ecology [5]. Further, because the Amazon and its tributaries are very dynamic – often changing their routes within a time span of a few decades [1,10] – it very well may be that forests that are unflooded today were flooded in the past and vice versa. This flooding dynamic then, along with differences in, at least, biota and soil characteristics [10,12], creates complex and diverse forest associations throughout the Amazon basin [9].

Therefore in order to better understand how Amazonian rainforests

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are structured, and to collect data urgently needed in the Neotropics for sound, sustainable management efforts, Iexpand on past sampling of Amazon flooded forests [13-16] by setting up and sampling a 1 ha plot in an Amazon igapó forest and a1 ha plot in an Amazon várzea forest. I then use that data to compile floristics in the igapó forest, and to compute several forest structure 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, in order to address these questions:

(1) What species, genera, and families (floristics) are found in this medium-flooded igapó forest?

(2) What is the physical structure of this igapó forestand the less-flooded várzeaforest?

(3) Which aspects of that structure are similar to other samplings of these types of forests, and which are not?

(4) Putting together this sampling and others can we begin to say how those similarities and differences relate to water quality (white vs. black) and the numbers of months of flooding/ maximum water depth, within each forest type?

(5) Are there patterns in how these parameters vary among permanent plot samplings of other Amazonigapó, várzea and *terra firme* forests, which suggest an effect of flooding on forest structure?

Methods

Study sites

The first study site is the Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: www.perujungle.com) [9,15,16] located in Loreto Province, 80 miles southeast of Iquitos, Peru (~2° S, 75° W) with an elevation of ~100 m a.s.l. The reserve is part of one of the largest protected areas in the Amazon, containing wet lowland tropical rainforest [17] of high diversity [3,18]. 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 [10]. 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 createigapó forests of differing frequency, duration, and maximum water column height, where the rainy season is between November and April [5]. Common tree species include *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata*, *Phytelephas macrocarpa* with under-story palms such as *Guazuma rosea*, and *Piptadenia pteroclada* [3,15,19,20].

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 [21-25]. Most of the YRS is *terra firme* forest which has been classified as lowland tropical rainforest [17]. The mean annual rainfall is 3081 mm with the wettest months April to May and October to November. August is the driest monthand 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 aluminium and iron, whereas soils at the station in *terra firme* forest are acidic and rich in exchangeable bases with a texture dominated by silt [8]. 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 [26], parts of which have been sampled [27-30]. 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.

Plot set-up and sampling

In May 2011, my field assistant and I set up a 1 ha plot in an igapó forest at the ACRCTT, which is underwater 3-4 months every year, and tagged and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in 10 m × 10 m continuous subplots. 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. Plots of this size have been used to study flooded forests in the Amazon for decades [31]. In June 2013, the tagged trees were identified to species, or to genus in a few cases, using Romoleroux et al. [32] and Gentry [33] as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana herbarium and the web site of the Missouri Botanical Garden <www.mobot.org>.

In May 2010, my field assistants and I set up a 1 ha plot next to the Tipitini River and a few hundred meters from the 50 ha *terra firme* plot [26]. We tagged, identified, and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in 10 m×10 m continuous subplots. The trees were identified using the same protocol as the plot at ACRCTT. This data is archived at the Luquillo Experimental Forest as LTERDBAS#172 as part of the LTER program funded by the US National Science Foundation. One may visit their website (http://luq.lternet.edu) for further details.

Data analysis

From the igapó data set I first compiled Floristic tables of family, genus and species. Then for both the igapó data set and the várzea data set I generated (1) the total number of stems in the 1 ha plot, the mean and maximum among those stems, and the total number of stems divided into 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 [34,35], (3) canopy closure using the formula in Buchholz et al. [36] for tropical treeswith 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 and Laurance [37] suggested for tropical trees of these stem sizes. A few years ago, other plots were also set up at ACRCTT in the same black-water flooded forest as the 1 ha plot and those results [9,15,16] create replication.

Results

There were a total of 16 families found in the 1 ha igapóplot (Table 1). Fabaceae was by far the most common family which also had the most genera and the most species. The families Moraceae, Annonaceae and Sapotaceae were also common, but there were 4 families with only one stem. The number of species was greater than or equal to the number of genera for every family. Dividing the stems by size class showed that most families have a monotonic decline in stem number as stems get thicker (Table 2). This was not true, however, of the families Elaeocarpaceae, Boraginaceae and Sapotaceae. The most

Family	total number of stems	No.of Genera	No., Of Species
Fabaceae	(62)	55	
Moraceae	(22)	44	
Annonaceae	(19)	23	
Sapotaceae	(19)	2	2
Chrisobalanaceae	(15)	33	
Rubiaceae	(9)	11	
Elaeocarpaceae	(5)	1	1
Malvaceae	(4)	2	2
Aquifoliaceae	(2)	1	1
Burseraceae	(2)	1	1
Combretaceae	(2)	1	1
Lamiaceae	(2)	1	1
Anacardiaceae	(1)	1	1
Boraginaceae	(1)	1	1
Rhizophoraceae	(1)	1	1
Salicaeae	(1)	1	1

Table 1: Each family sampled in the 1 ha igapóplot sorted in decreasing order by total number of stems (in parenthesis) followed by the total number of genera and the total number of species.

Family	10 < 19 cm	20 < 29 cm	30 < 39 cm	40 cm or greater
Fabaceae	62	28	2383	
Moraceae	22	11	722	
Annonaceae	19	10	72	0
Sapotaceae	19	7	453	
Chrisobalanaceae	15	10	50	0
Rubiaceae	9	5	40	0
Elaeocarpaceae	5	2	30	0
Malvaceae	4	22	0	0
Aquifoliaceae	2	2	0	0
Burseraceae	2	11	0	0
Combretaceae	2	11	0	0
Lamiaceae	2	2	0	0
Anacardiaceae	1	1	0	0
Boraginaceae	1	1	0	0
Rhizophoraceae	1	100	0	0
Salicaeae	1	100	0	0

Table 2: The family and total stems for each family from table 1 divided into size classes based on diameter at breast height (dbh) measured in whole cm.

common species were *Campsiandraangustifolia*, *Crudiaglaberrima*, and *Pseudolmedialaevigata* (Table 3).

The igapóstudy plot 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 total number of tree stems in the 1 ha plot – the stem density – was lower than the ranges sampled in other igapóforests which may have flooded less. The average dbh was slightly greater than the only other sample which reported it (in Brazil). It should be noted, however, that there were only half as many other samples for this forest compared to várzea. The trees were again clumped, but at a higher degree than the várzea forest. Canopy closure was only approx 12%, about half of the várzea forest. Basal area was also much less than both the other igapó sampling (in Brazil) and the várzea study plot. Above-ground biomass followed the same trend as basal area (Table 4).

The várzea study plot conformed to the reverse J stem size distribution pattern for stems less than 40 cm dbh, but had many more stems in the largest size class than expected included one of 80 cm dbh (Table 5). The total number of tree stems in the 1 ha plot – the stem density – was within the ranges sampled in other várzea forests, and close to the middle of the ranges. The average dbh was slightly greater than the only other sample which reported it (in Brazil). The trees were clumped, but at a low level (Table 5). Canopy closer was close to 45% and the basal area was again within the ranges of other várzea samplings, but at the lower end of that variation. Above-ground biomass was also lower than another várzea forest, sampled in Brazil to the east.

When comparing the two study plots which both received flooding, to unflooded samplings, we see a small reduction in average stem diameter (Table 6). In addition, there were more stems in the unflooded plots. 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.). Finally above-ground biomass was larger in *terra firme* compared to either flooded forest. The pie graphs reveal a “saddle” stem size distribution pattern for várzea (Figure 1a) and a more reverse J distribution pattern for igapó (Figure 1b).

Discussion

There was less than half the number of families in the 1 ha igapóplot compared to the 1 havárzeaplot (16 vs. 40: author, unpub. data). This could have been the result of poorer water quality or more flooding duration and maximum depth in the 1 ha igapóplot, or some other factor.There were nine familiesin common (out of 16), however. But no common genus or species were found between the two plots.

Family	Genus	species	number of stems
Annonaceae	Annona	montana Mac	7
Chrysobalanaceae	Couepia	subcordata Benth	5
Fabaceae	Crudia	glaberrima Mac	11
Fabaceae	Campsiandra	angustifolia Spruce	13
Moraceae	Pseudolmedia	laevigata Trecul	9
Rubiaceae	Genipa	spruceana Steyeermark	4
Sapotaceae	Sarcaulus	brasiliensis Eymaoppii	5

Table 3: All species in the 1 ha igapó plot with at least 4 stems, sorted by family, genus and species.

Parameter	Ecuador (at least 6)	Brazil1	Brazil2	Brazil3
Stems (dbh):				
10 < 19	84	--	--	--
20 < 29	58	--	--	--
30 < 39	17	--	--	--
40 or greater	8	--	--	--
mean	22.3	20.7	--	--
maximum	91	--	--	--
total	167	683	220-546	222
Dispersion:				
spatial pattern	clumped	-	-	-
green’s index	0.17	-	-	-
Canopy:		-	-	-
Closure (m^2)	1231.22	-	-	-
% ha closed	12.3122	-	-	-
Basal area (m^2)	6.52	31.4	-	-
AG biomass (Mg)	202	387.8	-	-

[1]Haugaasen and Peres 2006, [2]Ferreira 1997, [3]Campbell et. al. 1986

Table 4: Structural parameters for all trees at least 10 cm dbh sampled in Amazon igapóflooded forests, normalized per ha. The number of months underwater (when known) is indicated in parentheses for each plot.

Parameter	Ecuador (1-2)	Brazil1	Brazil(6)2	Brazil3	Ecuador4	Brazil5	Brazil(1-5)6
Stems (dbh):							
10<19	366	--	--	--	--	--	--
20<29	87	--	--	--	--	--	--
30<39	39	--	--	--	--	--	--
40 or greater	81	--	--	--	--	--	--
mean	24.2	22.1	--	--	--	--	--
maximum	80	--	--	--	--	--	--
total	573	515.3	560-745	423-612	417	420-777	370-466
Dispersion:							
spatial pattern	clumped	--	--	--	--	--	--
green's index	0.02	--	--	--	--	--	--
Canopy:		--	--	--	--	--	--
Closure (m2)	4478.04	--	--	--	--	--	--
% ha closed	44.7804	--	--	--	--	--	--
Basal area (m2)	26.356	29.6	17-45	-	35.5	25-27	31-48
AG biomass (Mg)	292	417.1	--	--	--	--	--

[1]Haugaasen and Peres 2006, [2]Worbes et. al. 1992, [3]Ferreira 1997, [4]Balslev et. al. 1987, [5]Campbell et. al. 1992, [6]Wittmann et. al. 2004b

Table 5: Structural parameters for all trees at least 10 cm dbh,sampled in Amazon várzeaflooded forests and normalized per ha. The number of months underwater, when known, is indicated in parentheses for each plot. Ranges and means are given when there are multiple samplings. The first listed plot is the study plot.

Parameter	igapóplotvárzea	plotTerra firme	plot1Terra firme	plot2Terra firme	plot3
Stems (dbh):					
10<19		84	366	--	--
20<29	58	87	--	--	--
30<39	17	39	--	--	--
40 or greater	8	81	--	--	--
mean	22.3	24.2	--	21.7	--
maximum	91	80	--	--	--
total		167	573	604 – 725	605.3734
Dispersion:					
spatial pattern	clumped	clumped	--	--	--
green's index	0.17	0.02	--	--	--
Canopy:					
Closure (m^2)	1231.22	4478.04	--	--	--
per ha (%)	12.3122	44.7804	--	--	--
Basal area (m^2)	6.52	26.356	22.2 – 31.2	32.6	22.2
AG biomass (Mg)		202292	--	457.8	--

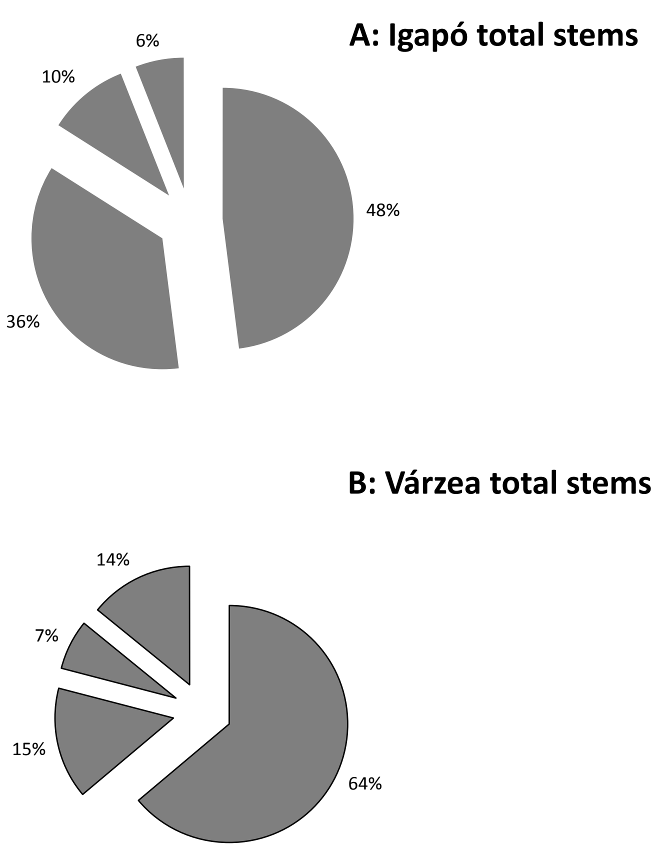
[1]Valencia et. al. 2004abc, [2]Haugaasen and Peres 2006, [3] Korning et. al. 1990

Table 6: Structural parameters for all trees at least 10 cm dbh sampled in the study igapóflooded forest, in the study várzea flooded forest, and in three *terra firme* forests. All data are expressed as per hectare.

The study plot in igapó forest was lower in stem density, basal area and AGB compared to other igapó samplings which may have been flooded for less time. For this study plot 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 *terrafirme* 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 plot in várzeaforest compared well to other várzea samplings in all regards except for low ABG. This study plot had more large stems than the reverse J distribution found in the 50 ha plot [27] and in *terra firme* forests within the Yasuni National Park [38] and at other Amazon sites [39]. This suggests that while smaller stems die from flooding, a stem may survive to a large size if it can reach a certain "threshold" size and take advantage of the resources that the dead stems are not now using. Consequently, the study 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 this plot (author unpub.data) that the seven most common families were also among the top ten families found in multiple samplings in the nearby 50 ha plot [27-29] 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 (author unpub. data).

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]: [author unpub.


A: Igapó total stems

B: Várzea total stems

Figure 1: Pie graph of total stems **(A)** in the 1 ha igapóflooded forest divided by stem size class: 10<19 cm (48%), 20<29cm (36%), 30<39cm (10%) and 40 cm or greater (6%), **(B)** in the 1 ha várzeaflooded forest divided by stem size class: 10 < 19 cm (64%), 20 < 29 cm (15%), 30 < 39 cm (7%) and 40 cm or greater (14%).

data] [15,16] tree stems and canopy coverage declined as flooding increased, more so than reductions due to tree fall, 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 tree fall where Amazonian forests may have gradients (flooding) and disturbances (tree fall) 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 tree fall 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[15,16] [author unpub. data].

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 [38]. 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 [9,40,41]. 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 [10]. The loss of tree stem density with flooding [13] 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 [42]. Clumping was less than that found in larger forest openings recovering from agriculture [35] 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 [16]. 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. Such studies will show that the underlying process of these forests, as for all plant communities, is plant-plant replacement [43]. These permanent plot studies, and others like them in the Amazon, 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.

Conclusion

The most obvious conclusion of these two samplings, and others done in the same forest types, is that flooding reduces forest structure. This can be seen in total stem density, basal area and ABG. 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 [9] 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 discover the causes of Amazon flooded forest structure.

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