

VÁRZEA FOREST VS. *TERRA FIRME* FOREST FLORISTICS AND PHYSICAL STRUCTURE IN THE ECUADOREAN AMAZON

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Abstract. I compared the floristic and physical structure of a white-water várzea flooded forest in the Amazon with a near-by unflooded *terra firme* forest. I set up and sampled a 1 ha plot in a white-water flooded forest, measuring and identifying every tree at least 10 cm diameter at breast height, which is close to a 50 ha plot in *terra firme* forest, maintained by the Smithsonian Institute's Tropical Forest Research program. I found that (1) the seven most common families sampled in the 1 ha plot were also among the top ten families sampled in the 50 ha plot, but most of the rare families were not, (2) at the genus and species taxonomic level, similarities with the 50 ha plot disappeared except for the genera *Cecropia*, *Alchornea*, *Inga*, *Zygia*, *Eschweilera* and *Virola* and the species *Iriarteia deltoidea* and *Coccoloba densifrons*, (3) the 1 ha plot lost stems with flooding but that loss was mainly in the smaller size classes leading to a proportionally greater number of larger trees than the *terra firme* forest and a larger basal area for stems at least 40 cm in diameter at breast height, and (4) because the flooded forest loses families, genera and species proportionally more than they lose stems, Fisher's α was lower in the flooded forest compared to *terra firme* forest.

Key words: Ecuador, LTER, Smithsonian, white-water, Yasuni

INTRODUCTION

The Amazonian rainforest encompasses over 6000000 km² (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 this rainforest influences the entire world's weather patterns and climate (Keller *et al.*, 2004) and may even control how much rainfall it itself receives (Pires & Prance, 1985). Perhaps most importantly for the future of humans the Amazonian rainforest interacts intimately with the Earth's carbon (C) cycle acting both as a carbon "sink", by taking in large amounts of CO₂ through photosynthesis, but also as a carbon "source" as, for example, when its plants decay or burn. This rainforest will continue to be a major C player in the future by both contributing to (through deforestation) and suffering 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, which share much structural similarity with unflooded rainforests throughout the rest of the Neotropics

(Kalliola *et al.*, 1991, Everham *et al.*, 1996, Pitman *et al.*, 2002, Myster 2009). Within that broad classification are types of *terra firme* which differ 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: Tuomisto *et al.*, 2003). The low relief of the Amazon basin leads to flooding which generates flooded forests covering at least 120000 km² (Parolin *et al.*, 2004). Flooding differs within the Amazon landscape in frequency, timing, duration, water quality, and maximum water depth and height (Tuomisto *et al.*, 2003) which is often correlated with duration (Junk & Piedade, 2010). Most of this water is the 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 (Junk, 1989).

The better studied várzea has light levels on the forest floor similar to *terra firme* (1-3% of ambient: Wittmann *et al.*, 2010) but flooding creates oxygen deficiency, reduced photosynthesis and low water conductance so that it may be a greater source of mortality than desiccation. In addition high nutrients within these disturbed forests can lead to trees with

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rapid growth rates and low wood densities. Further, trees within these forests must time their reproduction cycles in relation to the flooding; some grow mainly during the flooded times of the year and reproduce when the waters subside, others merely “endure” flooding and grow and reproduce only during the drier times of the year (Junk & Piedade, 2010).

Because the Amazon and its tributaries are very dynamic – often changing their routes within a time span of a few decades (Pires & Prance, 1985; Junk, 1989) – it may very well be that forests that are unflooded today were flooded in the past and *vice versa*. Indeed many *terra firme* species establish ecotypes (Myster & Fetcher, 2005) in the flooded forest (Witmann *et al.*, 2004, 2010). For example (1) the *terra firme* species *Guazuma ulmifolia* and *Spondias lutea* have developed flood-resistant ecotypes now found in várzea, (2) várzea species such as *Ceiba pentandra* and *Pseudobombax munguba* occur in *terra firme*, and (3) several species of the genus *Maquira* occur in both unflooded and flooded forests. In addition the predictability of the flood “pulse” – both past and present – facilitates adaptation and thus, along with differences in the surrounding biota and a variety of soil types (Junk, 1989; Honorio, 2006), creates complex and diverse forest associations throughout the Amazon basin (Myster, 2009).

In this study I expand on past sampling of Amazon flooded forests (Parolin *et al.*, 2004; Balslev *et al.*, 1987; Worbes *et al.*, 1992; Myster, 2007a, Myster, 2010) by setting up and sampling a 1 ha plot close to both (1) the white-water Tipitini river (a tributary of the Napo river) and (2) a 50 ha *terra firme* plot set up and sampled by the Smithsonian Tropical Research Institute. My goal is to explore the similarities and differences between the two forests and decide how white-water flooding changes floristic and physical structure of *terra firme*. Those differences may be in tree composition at the family, genus, or species taxonomic level, and/or in the common forest structure parameters of stem density, total basal area, family richness, genus richness, species richness, species evenness, and Fisher’s α .

METHODS

The study site is the Yasuni Research Station (YRS: 0o41’ S, 76o24’ W), operated by the Pontificia Universidad Católica de Ecuador and located within the Yasuni National park of eastern Ecuador (Myster, 2009, Duivenvoorder *et al.*, 2001, Myster & Santa-

cruz, 2005, Metz *et al.*, 2008, Myster 2012). Most of the YRS is *terra firme* forest which has been classified as lowland tropical rainforest (Holdridge, 1967). The mean annual rainfall is 3081 mm 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 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 (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, 2004) parts of which have been sampled (Valencia *et al.* 2004a, 2004b, 2004c, 2009). Also prevalent at YRS is floodplain forest – located next to the nutrient rich white-water Tipitini River – which is underwater off and on for a few weeks between the months of October and April to a maximum depth of 3 m.

In May and June of 2010, I set up a 1 ha plot in the YRS and next to the Tipitini river. The 1 ha plot was then subdivided into 100 continuous 10 x 10 m subplots, which provided replication. In each subplot I and my field assistants tagged, identified, and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh. Individual 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 on-site herbarium and the web site of the Missouri Botanical Garden <www.mobot.org>. The data are archived at the Luquillo Experimental Forest as LTERDBAS#172, part of the LTER program funded by the US National Science Foundation. One may visit their website (<http://luq.lternet.edu>) for further details. The 1 ha plot is located a few hundred meters from the 50 ha plot.

After tree identification was complete, I computed the total number of families, total number of genera and total number of species (richness) for the 573 stems sampled. I also computed species evenness, fisher’s α and basal area for comparison with four different samplings of western subplots of the 50 ha plot: (1) one ha of bottomland (Valencia *et al.*, 2004a), (2) one ha of ridge (Valencia *et al.*, 2004a), (3) the western 25 ha first census done in 1999 (Valencia *et al.*, 2004b; Valencia *et al.*, 2004c), and (4) the western 25 ha second census done in 2003

(Valencia *et al.*, 2009). I calculated an evenness index (E) based on Simpson's dominance index (Simpson, 1949: $E = (1 / \sum p_i^2) / S$, where p_i is the proportion of the total stems of species i and S is the number of species. The index ranges from 0 (all stems in one species) to 1 (all species having equal abundances (Mulder *et al.*, 2004) and is mathematically independent of species richness (Smith & Wilson, 1996). Fisher's α is defined by the formula: $S = \alpha \ln(1 + N/\alpha)$, where S = the number of species and N = the number of individual stems (Fisher *et al.*, 1943) and was computed using iteration. Total basal area (BA) is the sum of the basal areas of all individual stems where the BA for each stem = $\sum r^2$, where r is the dbh for each individual stem / 2. Basal area from dbh measurements is also a useful correlate of tree biomass (O'Brien *et al.*, 1995).

RESULTS

There were a total of 40 families found in the 1 ha plot (Table 1). Fabaceae was by far the commonest family and also had the most genera and the most species. The families Meliaceae, Cecropiaceae and Euphorbiaceae were also common, but 10 families were recorded 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 Fabaceae, Euphorbiaceae, Moraceae, and Sapotaceae which had a greater number of the largest stems (dbh at least 40 cm) compared with the next smaller class of stems.

The commonest species were *Guarea macrophylla* (41 stems), *Alchornea latifolia* (27 stems), *Cecropia membranacea* (25 stems), *Inga spectabilis* (23 stems) and *Macarobium acasifolium* (23 stems: see Table 3). Of the genera with at least four stems in the plot only two – *Cecropia* and *Inga* – had multiple species. When total stems are divided by stem size class, stems between 10 and 19 cm are 64% of the total, stems between 20 and 29 cm are 15% of the total, stems between 30 and 39 cm are 14% of the total, and stems 40 cm or greater are 7% of the total (Table 4). Stem evenness shows that the distribution of stems became more even as stem size increases but, again, not at the largest stem size class. Fisher's α conforms to a steep decline with increasing stem size, but total basal area shows a much larger BA in the larger stem size class.

Total stems were reduced after flooding compared with all four samplings of the 50 ha *terra firme* plot (averaged to 1 ha: Table 5) but not to a great degree. Total families, total genera and total species were all greater in *terra firme* compared with the flooded forest, but there is some variation in species richness among the *terra firme* samplings. Species evenness was not computed in any of the four samplings of the 50 ha plot. Fisher's α follows the same trend as species richness but with less variation among the *terra firme* samplings. Total basal area was, however, greatest in várzea (after flooding) suggesting that it is the smaller stems that die from flooding allowing the remaining trees to grow larger.

DISCUSSION

The seven most common families sampled in the 1 ha plot were also among the top ten families sampled in the 50 ha plot located on-site in *terra firme* (for stems sampled down to 1 cm dbh). Most of the families, especially the rare families, in the 1 ha plot were not found in the *terra firme* plot. There was also good numerical association for stems > 30 cm dbh (27 families in flooded forest per ha vs. 24 families in *terra firme* forest, 36 vs. 41 genera, 48 vs. 55 species).

Among samplings of similar flooded forests in Peru (Godoy *et al.*, 1999, Honorio, 2006, Myster, 2007a, Wittmann *et al.*, 2010) the families Fabaceae, Euphorbiaceae, Lecythidaceae, Urticaceae, Arecaceae and Moraceae were also common. In the 1 ha plot sampled in this paper all families (except Fabaceae, Cecropiaceae, and Euphorbiaceae) had more stems in the smallest size class compared with the other size class. Perhaps the larger trees in these three families can take advantage of the increase in space, nutrients and light – after flooding kills the smaller stems (Junk & Piedade, 2010) – more than individual trees of other families. There are also tree seedling and sapling physical damage vectors in addition to flooding (reviewed in Myster, 1993). Results suggest that for stems in these three families (Fabaceae, Cecropiaceae, Euphorbiaceae) there may be a “threshold” stem size that they must reach to survive and grow.

When we look at the genus and species taxonomic level, similarities between the 1 ha plot sampling and the 50 ha plot samplings disappear (though there was 25% - 32% similarity between these forest types in central Amazonia: Wittmann *et al.*, 2010). There were, however, many genera present in the 1 ha plot that were common in other samplings of similar forests in central Amazonia (*Guarea*, *Pouteria*,

TABLE 1. Each family sampled in the 1 ha plot 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 (total number of stems)	Total number of genera	Total number of species
Fabaceae(125)	9	25
Meliaceae(45)	2	5
Cecropiaceae(44)	2	3
Euphorbiaceae(36)	5	8
Lecythidaceae(31)	3	7
Bombacaceae(27)	4	6
Moraceae(23)	7	8
Arecaceae(21)	6	7
Melastomataceae(20)	3	12
Bixaceae(18)	1	1
Vochysiaceae(16)	2	2
Annonaceae(15)	3	5
Flacourtiaceae(15)	3	6
Nyctaginaceae(15)	1	1
Sapotaceae(14)	2	6
Myristicaceae(12)	1	3
Sapindaceae(11)	2	5
Chrysobalanaceae(10)	2	5
Rubiaceae(10)	6	6
Lauraceae(8)	4	6
Clusiaceae(7)	2	4
Burseraceae(5)	3	6
Polygonaceae(4)	2	2
Sterculiaceae(4)	2	2
Apocynaceae(3)	2	3
Simaroubaceae(3)	1	2
Elaeocarpaceae(2)	1	2
Olacaceae(2)	1	1
Picramniaceae(2)	1	2
Sabiaceae(2)	2	2
Violaceae(2)	1	2
Anacardiaceae(1)	1	1
Bignoniaceae(1)	1	1
Combretaceae(1)	1	1
Dichapetalaceae (1)	1	1
Ebenaceae(1)	1	1
Icacinaceae(1)	1	1
Myrtaceae (1)	1	1
Ochnaceae(1)	1	1
Opiliaceae(1)	1	1
Ulmaceae(1)	1	1

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.

Family	10 < 19 cm	20 < 29 cm	30 < 39 cm	40 cm or greater
Fabaceae(125)	7	27	11	14
Meliaceae(45)	33	4	4	4
Cecropiaceae(44)	11	14	9	10
Euphorbiaceae(36)	19	6	3	8
Lecythidaceae(31)	18	7	4	2
Bombacaceae(27)	27	0	0	0
Moraceae(23)	20	0	0	3
Arecaceae(21)	16	2	2	1
Melastomataceae(20)	17	1	1	1
Bixaceae(18)	18	0	0	0
Vochysiaceae(16)	10	6	0	0
Annonaceae(15)	8	4	0	3
Flacourtiaceae(15)	12	2	1	0
Nyctaginaceae(15)	15	0	0	0
Sapotaceae(14)	8	1	1	4
Myristicaceae(12)	7	3	1	1
Sapindaceae(11)	6	4	0	1
Chrysobalanaceae(10)	5	2	1	2
Rubiaceae(10)	9	1	0	0
Lauraceae(8)	8	0	0	0
Clusiaceae(7)	7	0	0	0
Burseraceae(5)	3	1	1	0
Polygonaceae(4)	4	0	0	0
Sterculiaceae(4)	1	3	0	0
Apocynaceae(3)	2	0	1	0
Myrtaceae (3)	3	0	0	0
Simaroubaceae(3)	2	0	0	1
Elaeocarpaceae(2)	2	0	0	0
Olacaceae(2)	2	0	0	0
Picramniaceae(2)	2	0	0	0
Sabiaceae(2)	2	0	0	0
Violaceae(2)	2	0	0	0
Anacardiaceae(1)	0	0	1	0
Bignoniaceae(1)	1	0	0	0
Combretaceae(1)	1	0	0	0
Dichapetalaceae(1)	1	0	0	0
Ebenaceae(1)	1	0	0	0
Icacinaceae(1)	1	0	0	0
Myrtaceae(1)	1	0	0	0
Ochnaceae(1)	0	1	0	0
Opiliaceae(1)	1	0	0	0
Ulmaceae(1)	0	0	0	1

TABLE 3. All species with at least 4 stems sorted by family, genus and species.

Family	Genus	Species	Number of stems
Annonaceae	<i>Duguetia</i>	<i>spixiana</i>	7
Annonaceae	<i>Xylopia</i>	<i>ligustrifolia</i>	8
Arecaceae	<i>Euterpe</i>	<i>precatoria</i>	10
Arecaceae	<i>Iriartea</i>	<i>deltoidea</i>	6
Bixaceae	<i>Bixa</i>	<i>urucurana</i>	18
Bombacaceae	<i>Quararibea</i>	<i>wittii</i>	20
Cecropiaceae	<i>Cecropia</i>	<i>latiloba</i>	14
Cecropiaceae	<i>Cecropia</i>	<i>membranacea</i>	25
Chrysobalanaceae	<i>Licania</i>	'zigzag'	5
Clusiaceae	<i>Vismia</i>	<i>baccifera</i>	4
Euphorbiaceae	<i>Alchornea</i>	<i>latifolia</i>	27
Euphorbiaceae	<i>Sagotia</i>	<i>racemosa</i>	4
Fabaceae	<i>Inga</i>	<i>alata</i>	13
Fabaceae	<i>Inga</i>	<i>cinnamomea</i>	7
Fabaceae	<i>Inga</i>	<i>leiocalycina</i>	16
Fabaceae	<i>Inga</i>	<i>nobilis</i>	9
Fabaceae	<i>Inga</i>	<i>spectabilis</i>	23
Fabaceae	<i>Inga</i>	'Zalangosta'	4
Fabaceae	<i>Macrolobium</i>	<i>angustifolium</i>	23
Fabaceae	<i>Zygia</i>	<i>grandiflora</i>	6
Flacourtiaceae	<i>Casearia</i>	<i>uleana</i>	5
Flacourtiaceae	<i>Laetia</i>	<i>procera</i>	5
Lecythidaceae	<i>Eschweilera</i>	<i>tessmannii</i>	24
Meliaceae	<i>Guarea</i>	<i>macrophylla</i>	41
Moraceae	<i>Sorocea</i>	<i>steinbachii</i>	7
Myristicaceae	<i>Virola</i>	<i>surinamensis</i>	8
Nyctaginaceae	<i>Neea</i>	'pantano'	20
Sapindaceae	<i>Cupania</i>	<i>scrobiculata</i>	4
Sapotaceae	<i>Pouteria</i>	'angostaloopy'	5
Vochysiaceae	<i>Vochysia</i>	<i>braceliniae</i>	15

TABLE 4. Basic structural parameters of the 1 ha plot divided by stem size class.

parameter	10 < 19 cm	20 < 29 cm	30 < 39 cm	40 cm or greater
total stems	366	87	39	81
total families	41	17	13	14
total genera	78	27	17	19
total species	134	45	22	26
species evenness	0.61	0.69	0.71	0.55
fisher's α	76.1	40.5	20.2	14.4
total basal area	5.395m ²	3.218m ²	3.438m ²	19.950 m ²

TABLE 5. Basic structural comparison of the 2010 sampling of the 1 ha flooded forest plot with four samplings of western subplots of the 50 ha plot: (1) one ha of bottomland¹, (2) one ha of ridge¹, (3) the western 25 ha first census in 1999^{2,3}, and (4) the western 25 ha second census in 2003⁴. All data are expressed as per hectare. In the case of the 50 ha plot this means that data were averaged over the entire sampling. N/A means that data were either not computed, not published and/or unavailable for some other reason.

	flooded forest	bottomland	ridge	1999 census	2003 census
total stems	573	604	725	702	698
total families	40	N/A	N/A	47	N/A
total genera	98	N/A	N/A	132	N/A
total species	185	234	255	251.4	N/A
species evenness	0.63	N/A	N/A	N/A	N/A
fisher's α	95.2	140.2	140.0	147.6	N/A
total basal area	32.013 m ²	22.2 m ²	31.2 m ²	27.4 m ²	N/A

¹ Valencia *et al.* 2004a; ² Valencia *et al.* 2004b; ³ Valencia *et al.* 2004c; ⁴ Valencia *et al.* 2009

Eschweilera, *Inga* and *Duguetia*: Wittmann *et al.*, 2010). For example, *Iriartea deltoidea* was the only species in common between the 1 ha plot, and the ridge subplot, the bottomland subplot and the western 25 subplots which are all different parts of the 50 ha plot (Valencia *et al.*, 2004a; 2004b) except for *Coccoloba densifrons* which was also present in the 1 ha plot (Valencia *et al.*, 2004b). A few genera, however, were common in both plots (*Cecropia*, *Lachornea*, *Inga*, *Zygia*, *Eschweilera* and *Virola*). There was more similarity between the 1 ha plot and a previous sampling of this kind of flooded forest in Peru (Myster, 2007a) where species of the genera *Duguetia*, *Licania*, *Virola* and *Pouteria* were found. In general, this 1 ha plot had little taxonomic similarity at the species level with either the nearby *terra firme* or more eastern Amazonian várzea forests (Wittmann *et al.*, 2010).

When we combine all the families together, we again see more, larger individuals than expected primarily in the common families given listed earlier. This differs from both samplings of the western half of the 50 ha plot where stem density in the 20 - 30 cm dbh size class was 138 and 137 stems/ha and 81.4, 84 stems/ha in the over 30 cm dbh size class (Valencia *et al.*, 2009). The kind of flooded forest sampled here had larger individuals than *terra firme* in another study (Korning & Balslev 1994). Similar stem densities in the > 30 dbh size class were seen in ridge plot (105 stems/ha and 64 species/ha), bottomland plot (62 stems/ha and 46 species/ha) and also in the western half of the 50 ha plot (81 stems/

ha and 41 species/ha: Valencia *et al.* 2004b; 2009). The decline in the other size classes with increasing size is closer to the steep, more exponential, decline seen in the 50 ha plot (Valencia *et al.*, 2004a) and other *terra firme* forests in the Yasuni National Park (Pitman *et al.*, 2002).

Total families, total genera and total species were all greater in *terra firme* compared with the flooded forest (Wittmann *et al.*, 2010). However with the greater reduction of stem numbers compared with the reduction of species in the 1 ha plot, it is no surprise that species evenness increases as stems get larger, except in the largest size class, suggesting that there are some very large trees in the flooded forest. Even so, evenness was larger in *terra firme* forests both in eastern (0.75-0.92) and southeastern Brazil (0.85-0.87). Fisher's α followed the species trends within the 1 ha forest but, for stems > 30 cm dbh, was smaller than the ridge plot (69.6), the bottomland plot (80.7), and the first western 25 ha sampling (88.5). Because the loss of stems after flooding is less proportional than the loss of species, the reduction in Fisher's α after flooding is most likely due to the loss of those families with few stems. Fisher's α is higher here, however, than more eastern várzea forests (Wittmann *et al.*, 2010). Basal area shows the influence of the large individuals because a decrease in stem numbers is offset with larger stems. In particular for the larger stems > 30 cm, basal area in the flooded forest was larger than the Ridge plot (16.6 m²/ha), the bottomland plot (9.1 m²/ha) and the western 25-ha first sampling (13.4 m²).

When we compare the structure of the 1 ha plot with the 50 ha plot all four samplings of the 50 ha plot have more stems and so there was a loss of stems with flooding. Similarly a sampling of 15 other unflooded forests (all stems at least 10 cm dbh) in Yasuni National Park (Pitman *et al.* 2002) showed an average of 654 stems per ha. The reduction, however, was not large where for one sampling the difference is only a couple of dozen of stems. The number of families is also reduced by flooding, but the reduction was greater for genera and species, which leads to a large reduction in Fisher's α after flooding. Numbers of genera and species were also reduced in the flooded forest (Wittmann *et al.*, 2010). The other 15 unflooded forests in Yasuni National Park (Pitman *et al.*, 2002) had on average 47 families, 129 genera and 239 species for stems > 10 cm with *Iriartea deltoidea* as the most common species. Total basal area is comparable among the flooded forests and the 50 ha plot because the flooded forest makes up in size what it loses in numbers. In select subplots within the 50 ha plot, tree seedlings (no taller than 50 cm) density was approximately nine per m² (Metz *et al.*, 2002).

In other samplings of this kind of flooded forest for stems of at least 10 cm dbh there were: (1) 417 stems/ha (Balslev *et al.*, 1987) and 500 stems/ha (Worbes *et al.*, 1992) – low compared with this plot – (2) 149 species/ha, ~100.8 species/ha in Amazonia but 120-160 species/ha in western Amazonia (Wittmann *et al.*, 2010) and 88 species/ha (Worbes *et al.*, 1992) – also low – and (3) 35.5 m² of basal area/ha (Balslev *et al.*, 1987) and 4.8 m² of basal area/ha (Worbes *et al.*, 1992) – comparable to this plot. In my own sampling of similar 125 m² plots in Peru (compared with the 10,000 m² in a 1 ha plot), species richness was 25, genera richness was 23 and fisher's α was 140 (Myster, 2010). Data suggests that the YRA flooded forest is denser and more species rich compared with other similar flooded forests, so flooded forests may share these and other characteristics with nearby *terra firme* forest, if there is one.

Because this forest is only under water a few weeks per year, it probably regenerates when not flooded just like the neighboring *terra firme* forest (Wittmann *et al.* 2010). Regeneration experiments done in the 1 ha plot – when unflooded and before it was laid out and sampled as a plot (author, unpublished data) – have suggested that seed rain, seed predation and competition are key regeneration mechanisms. Due to the flooding, however, compe-

titition for water may not be as critical in the 1 ha plot as it was in the YRS *terra firme* forest where I found variation in water availability was more important than light in determining tree seedling survivorship, growth and allocation along the forest floor. This could mean that trees in flooded forests differ more along light gradients than trees in *terra firme*, and that consequently, light is more important in defining their life histories supporting the traditional view of tropical forests (Bazzaz & Pickett, 1980). Those life histories must include, however, the tolerance of seedlings to flooding, critical in determining adult distribution and abundance (Grubb 1997, Parolin *et al.*, 2004).

Indeed, flooded forest species may be better competitors during the flooded phase than *terra firme* species but drought may be more harmful than waterlogging or even submergence and in addition more important than light during the non-flooded phase (Myster, 2010). Indeed flooding may offer some release from competition and, thus, facilitation may be more likely in flooded forests (and after agriculture: Myster 2007b) compared with *terra firme* (Balslev *et al.*, 1987). One of the common species found in the 1 ha plot, *Cecropia latiloba*, has been well-studied and found to be a fast-growing “pioneer” species with – high maxima CO₂ assimilation, quantum yield, and chlorophyll *a* fluorescence (Parolin *et al.*, 2010) – which may reduce its physiological activities due the few weeks of flooding at Yasuni. However its high germination rate may be a reason why it is common.

For tree composition the flooded forest had many of the same families as *terra firme*, but not at the genus and species taxonomic level. Studies suggest then that flooded forests have a unique biology and ecology where the regularity of flooding has led to the evolution of specific traits which combine with flooding to create tree species distributions (Parolin *et al.*, 2004). 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” shape than a monotonic decline in numbers with increasing size, as seen in the basal area. In addition because flooded forests lose families, genera and species more than they lose stems, fisher's α was reduced compared to unflooded *terra firme*. Although other studies have presented data which shows differences between *terra firme* forest and flooded forest in the Amazon, those forests were often

not located in close proximity to each other and, consequently, other environmental variables and sources of variation may have influenced any differences. Here at the YRS, because the two forests are located so close to each other, we can make a stronger case for the uniqueness of flooded forests.

Finally the fact that forests, whether flooded or unflooded, become more diverse as you move west across Amazonia implies at least two things: (1) that *terra firme* forest and várzea forest will be less similar in the western Amazon than elsewhere (as seen here), and (2) there will be a greater diversity not just within forests but also between them in the western Amazon and with more different forest types and plant associations. Perhaps differences in the flooding regime are a major reason why Amazonian, and particularly western Amazonian, forests are so diverse. For this várzea forest in western Amazonia, as I show here, it does not take that much flooding – the 1 ha plot may be underwater for only a few weeks per year on average – as long as the flooding is regular enough, to create significant differences in biodiversity and structure.

ACKNOWLEDGEMENTS

I thank Milton Zambrano Reyes, Anellio Loor and the staff at the Yasuni Research station. I also thank Henry Balslev, Stephen Roxburgh, Marco Tschapka and Marcel Holyoak for commenting on an earlier draft of the manuscript and Eda Melendez for managing the dataset. Finally I thank P.U.C.E. professors Rommel Montufar, Hugo Navarrete and Renato Valencia for their continuing support.

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