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Effects of Soil Type on Floristics and Stand Structure in Amazon Unflooded Forests

Randall W. Myster[1]

[1]Biology Department, Oklahoma State University, Oklahoma City, OK. 73107, USA

Correspondence: Randall W. Myster, Biology Department, Oklahoma State University, Oklahoma City, OK. 73107, USA. E-mail: myster@okstate.edu

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Abstract

The importance of unflooded forests in the Amazon and the need to investigate how their soils affect their floristics and stand structure, lead me to set up and sampled trees in four plots in *terra firme* forest, in white sand forest and in palm forest at the same site in the Peruvian Amazon. I found (1) the white sand forest plot had 15 families with Clusiaceae, Malvaceae and Myrtaceae the most common and *Pachira brevipes* the most common species, (2) the palm forest plot had 6 families with Arecaceae, Clusiaceae and Fabaceae the most common and *Socratea exorrhiza* the most common species, and (3) the *terra firme* forest plot had 47 families with Myristicacea, Fabaceae and Bombacace the most common and *Otoba parvifolia* and *Astrocaryum murumura* the most common species. For the stand structure of these forests, (1) *terra firme* had more stems and larger stems than white sand and palm, and while palm had more stems than white sand, white sand had larger stems than palm, (2) species richness was greatest in *terra firme* and decreased by a factor of three in white sand, and by a factor of five in palm, (3) basal area decreased from *terra firme* to white sand, but white sand and palm were comparable, (4) white sand had the greatest above-ground biomass, followed by *terra firme* and palm, and (5) white sand and palm were much more open forests than *terra firme*. Results strongly suggest that soils are a significant causal factor in determining floristic and structural differences among these Amazon forests, where the richer soil of *terra firme* forest helps produce both more structure and a richer floristics compared to the poor soil of palm forests and the even poorer soil of white sand forests.

Keywords: palm forest, Peru, Sabalillo Forest Reserve, *terra firme* forest, white sand forest

1. Introduction

Plant communities in the Amazon are among the most critical ecosystems to life on earth (Walter, 1973). They are the most productive (Daly and Prance, 1989) and diverse forests (Pires and Prance, 1985), and influence worldwide weather patterns and climate (Keller *et al.*, 2004). They are also key to the functioning of the earth's biogeochemical cycles. For example, in the Carbon cycle these rainforests act as a large carbon "sink" when they take in large amounts of CO_2 through photosynthesis, and a large carbon "source" when their trees decay or burn. The majority of Amazonian rainforests are unflooded, even though they are located in areas lower than 100 m elevation above sea level. The three most common of these unflooded forests differ fundamentally in their soils (1) *terra firme* forests found on clay or loam soils, (2) white sand forests on soils with a large amount of quartz (leading extremely infertile soils with low pH and low water retention capacity: Ruokolainen *et al.*, 1997), and (3) palm forests on standing water or water-logged clay (Terborgh and Andresen, 1998; Tuomisto *et al.*, 2003).

Terra firme forests share much of their stand structure with unflooded rainforests throughout the rest of the Neotropics (Kalliola *et al.*, 1991; Everham *et al.*, 1996; Pitman *et al.*, 2001; Tuomisto *et al.*, 2003). Palm forests occur in depressions and low-lying areas of poor drainage (Svenning, 1999a; Pitman *et al.*, 2014), and have a canopy of 12-30 m with arborescent palms and other trees (Myster, 2009). White sand forests have a shorter canopy with a lighter understory than *terra firme* forests (Medina and Cuevas, 1989) and a flora rich in endemics (Frasier *et al.*, 2008) where herbivory defense is a major factor in defining and differentiating among their tree species (Fine *et al.*, 2004; Fine *et al.*, 2006). Compared to *terra firme* forests, both white sand forests and palm forests are under significant stress (Fine *et al.*, 2010; Pitman *et al.*, 2014; Myster, 2016b) due to soil nutrient deficiency (in the case of white sand forest) or being water-logged and having O_2 deficiency (in the case of palm forest: Myster, 2017c).

Whereas Amazon soils can affect species distributions, and community floristics and stand structure (Ruokolaimen *et al.,* 2007), soil differences among unflooded Amazon forests in particularly allow an investigation into how Amazon soils affect forest floristics and stand structure. Consequently I expand on past sampling of these types of unflooded Amazon forests (Svenning, 1999a; Vormisto *et al.,* 2000; Honorio, 2006; Montafar and Pintaud, 2006; Normand *et al.,* 2006; Pitman *et al.*, 2008; Fine *et al.,* 2010) by setting up and sampling four plots in a *terra firme* forest, four plots in a white sand forest, and four plots in a palm forest. Unique to this study, however, all plots are at the same study site and within 100 m of each other, which increases the probability that any differences in floristics and stand structure are due to edaphic variation. I then use the plot data to address these three questions (1) What species, genera, and families are found in *terra firme* forest, in white sand forest, and in palm forest, all common unflooded forests in the Amazon?, (2) What is the stand structure of those forests? and (3) What do the results suggest about how the edaphic conditions of these forests may affect their floristics and stand structure?

2. Methods

2.1 Study Area

The study was conducted at Sabalillo Forest Reserve (SFR: 3^o 20’ 3”S, 72^o 18’ 6” W: Frederickson *et al.,* 2005; Moreau, 2008), was established in 2000 and is operated by Project Amazonas (www.projectamazonas.org). SFR is located on both sides of the upper Rio Apayacu, 172 km east of Iquitos, Peru. The reserve is part of 10,117 ha set aside over the last decade. Annual precipitation is 3.297 m per year (Choo *et al.*, 2007) and the rainy season is between November and April. All three study forests are common at SFR: white sand forest on soils of extreme infertility made up mainly of quartz podzols, palm forest on standing water with clay soils, and *terra firme* forest on loam soils.

2.2 Plot Set-up and Sampling

In June 2013, two local student field assistants and I set up four (50 m x 50 m) plots in *terra firme* forest, four (50 m x 50 m) plots in white sand forest, and four (50 m x 50 m) plots in palm forest, in 12 separate stands at SFR at typical locations suggested by the field assistants. All plots are located in the same study area and were at least 50 m apart. Consequently, while other studies could only suggest that these soils are influencing floristics and stand structure in these forests, I can make a stronger argument because effects of other potential causal factors (e.g., climate, rainfall, temperature) are in common among all the plots. We measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in each of the 12 plots. 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 forest floristics and structure in the Amazon for decades (see Myster, 2009 and chapters in Myster, 2017a; Myster, in press) and past publications using data from the *terra firme* plots (Myster, 2016b) have shown them to be typical of *terra firme* forests sampled by others in Western Amazonia. Trees were also 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 in Iquitos and the web site of the Missouri Botanical Garden <www.mobot.org>.

2.3 Data Analysis

Using the collected data, I first compiled floristic tables of family, genus and species for each forest after combining their four plots into a single 1 ha plot. I then generated, for each forest (1) the total number of stems, the mean dbh among those stems, and the total number of stems divided into four size classes: 10 < 20 cm dbh, 20 < 30 cm dbh, 30 < 40 cm dbh and ≥ 40 cm dbh, (2) species richness, (3) total basal area (the sum of the basal areas of all individual stems which is $\pi*r^2$ where r = the dbh of the individual stem / 2), (4) above-ground biomass (AGB) using the formula in Nascimento and Laurance (2001) suggested for Amazonian trees of these stem sizes and (5) canopy closure using the formula in Buchholz *et al.,* (2004) for tropical trees with the resulting percentage of the combined 1 ha plot area closed.

3. Results and Discussion

3.1 Floristics

There were 47 families found in the *terra firme* plot (Table 1) and Myristicacea was the most common family with Fabaceae and Bombacace common as well. There were 17 families with only one stem. There were 15 families found in the white sand plot (Table 1). Clusiaceae was by far the most common family, which also had the most genera and the most species. Malvaceae, Myrtaceae and Rubiaceae were also common, and there were two families (Arecaceae, Moraceae) with only one stem. There were six families found in the palm plot (Table 1). Arecaceae was by far the most common family, which also had the most genera and the most species. Clusiaceae, Fabaceae and Lecythidaceae were also common, and there was only one family (Opiliaceae) with only one stem. White sand forest had only four families with stems in palm forest but 15 families with stems in *terra firme* forest. Palm forest had only five families with stems in *terra firme* forest (Table 1).

Table 1. All families found in the white sand, palm and *terra firme* combined 1 ha plots sorted alphabetically with the number of tree stems sampled given under each forest-type

Family	white sand	palm	*terra firme*
Anacardiaceae	0	0	4
Annonaceae	11	0	36
Apocynaceae	0	0	1
Araliaceae	0	0	2
Arecaceae	1	235	30
Bignoniaceae	0	0	1
Bombacace	0	0	50
Boraginaceae	0	0	4
Burseraceae	23	0	18
Capparidacea	0	0	1
Caricaceae	0	0	3
Cecropiacea	0	0	5
Chrysobalanaceae	0	0	9
Clusiaceae	127	98	1
Dichapetalaceae	0	0	1
Elaeocarpaceae	3	0	1
Euphorbiaceae	3	8	18
Fabaceae	7	57	55
Flacourtacea	0	0	7
Humiviaceae	0	15	0
Icacinaceae	5	0	1
Lauraceae	0	0	19
Lecythidacea	0	36	18
Malpighiacea	0	0	1
Malvaceae	86	0	0
Melastomataceae	0	0	1
Meliaceae	0	0	22
Memecyle	0	0	1
Moraceae	1	0	22
Myristicacea	0	0	56
Myrtaceae	64	0	6
Nyctaginaceae	0	0	9
Olacaceae	0	0	1
Opiliaceae	0	1	0
Polygonaceae	0	0	4
Quiinaceae	0	0	1
Rhizoporaceae	0	0	1
Rubiaceae	48	0	4
Sabiaceae	0	0	1
Sapindaceae	10	0	2
Sapotaceae	3	0	42
Simaroubaceae	0	0	1
Siparunaceae	9	0	4
Staphyleaceae	0	0	1
Sterculiaceae	0	0	17
Tiliaceae	0	0	8
Ulmaceae	0	0	6
Urticaceae	0	0	3
Verbenace	0	0	1
Violaceae	2	0	4
Vochysiaceae	16	0	0

The most common species in *terra firme* forest were *Otoba parvifolia* and *Astrocaryum murumura*, in white sand forest *Pachira brevipes* and *Caraipa tereticaulis*, and in palm forest *Socratea exorrhiza* and *Lepidocaryum tenue* (Table 2). Among those most common species only one genera (Caraipa) and one species (*Oenocarpus bataua*) were found both in white sand forest and in palm forest. There were two genera in common between palm forest and *terra firme* forest (Astrocaryum, Eschweilera) but no species in common between *terra firme* forest and either white sand forest or palm forest (Table 2).

Table 2. All species in the combined 1 ha white sand plot, in the combined 1 ha palm plot and in the combined 1 ha *terra firme* plot, with at least 4 stems and sorted by family first, then genus and finally species

white sand forest plot			
Family	Genus	Species	number of stems
Arecaceae	Oenocarpus	bataua	4
Clusiaceae	Calophyllum	brasiliense	5
Clusiaceae	Caraipa	tereticaulis	15
Clusiaceae	Haploclathra	cordata	7
Clusiaceae	Tovomita	calophyllophylla	9
Fabaceae	Dicymbe	puncticulosa	8
Fabaceae	Macrolobium	microcalyx	5
Fabaceae	Tachigali	paniculata	9
Malvaceae	Pachira	brevipes	19
Sapindaceae	Cupania	diphylla	4
palm forest plot			
Family	Genus	Species	number of stems
Arecaceae	Astrocaryum	javarense	8
Arecaceae	Euterpe	precatoria Mart.	8
Arecaceae	Geonoma	macrostachys Mart. var. acaulis	14
Arecaceae	Lepidocaryum	tenue Mart. var. tenue	31
Arecaceae	Mauritia	flexuosa	9
Arecaceae	Oenocarpus	bataua	25
Arecaceae	Socratea	exorrhiza	44
Clusiaceae	Caraipa	valioi	5
Euphorbiaceae	Hura	crepitans	4
Fabaceae	Crudia	glaberrima	4
Lecythidaceae	Eschweilera	bracteosa	7
terra firme forest plot			
Family	Genus	Species	number of stems
Annonaceae	Unonopsis	floribunda	4
Arecaceae	Astrocaryum	murumura	20
Arecaceae	Iriartea	deltoidea	15
Bombacacea	Eriotheca	macrophylla	4
Bombacacea	Matisia	bracteolosa	6
Bombacacea	Matisia	malacocalyx	8
Bombacacea	Matisia	ochrocalyx	6
Bombacacea	Pachira	insignis	4
Bombacacea	Quararibea	loretoyacuensis	6
Burseracea	Protium	amazonicum	4
Burseracea	Tetragastris	panamensis	5
Cecropiacea	Cecropia	sciadophylla	4
Chrysobalanaceae	Licania	macrocarpa	5
Euphorbiacea	Nealchornea	yapurensis	6
Fabaceae	Bauhinia	brachycalyx	5
Fabaceae	Erythrina	poeppigiana	4
Fabaceae	Inga	oerstediana	9
Fabaceae	Platymiscium	stipulare	5
Fabaceae	Pseudopiptadenia	suaveolens	6
Lecythideacea	Eschweilera	gigantean	5
Meliaceae	Carapa	guianensis	4
Meliaceae	Guarea	kunthiana	4
Moraceae	Perebea	xanthochyma	7
Moraceae	Pseudolmedia	laevis	7
Myristicacea	Iryanthera	paraensis	8
Myristicacea	Otoba	glycicarpa	11
Myristicacea	Otoba	parvifolia	23
Nyctaginacea	Neea	spruceana	5
Sapotaceae	Pouteria	krukovii	5
Siparunacea	Siparuna	cristata	4
Tiliaceae	Apeiba	aspera	4
Urticaceae	Urera	caracasana	6
Violaceae	Leonia	glycycarpa	4

3.2 Stand Structure

Terra firme had more stems and larger stems than white sand and palm, and while palm had more stems than white sand, white sand had larger stems than palm (Table 3). For all three forests, stems conformed to a “reverse J” size distribution pattern. Species richness was greatest in *terra firme* and decreased by a factor of three in white sand, and by a factor of five in palm. Basal area decreased from *terra firme* to white sand, but white sand and palm were comparable. White sand had the greatest above-ground biomass, followed by *terra firme* and palm. White sand and palm were much more open forests than *terra firme* (Table 3).

Table 3. Stand structure parameters for all trees at least 10 cm dbh sampled in the combined 1 ha plots

parameter	white sand	palm	terra firme
Stem density:			
Total	403	449	519
10 < 20 dbh	241	253	288
20 < 30 dbh	95	176	121
30 < 40 dbh	63	20	50
40 or greater	3	0	60
mean dbh	19.8	14.1	20.8
Species richness	103	57	302
Basal area (m^2)	12.52	11.15	17.6
Above-ground biomass (Mg)	387.7	267.1	334.2
Canopy:			
Closure (m2)	1441.2	2356.7	6921.4
per ha (%)	14.412	23.567	69.214

While edaphic conditions have been suggested as causal factors in determining floristic and structural differences among these three Amazon forest-types before (Svenning, 1999a; Vormisto *et al.*, 2004; Honorio, 2006; Montafar and Pintaud, 2006; Normand *et al.*, 2006; Pitman *et al*., 2008; Fine *et al.*, 2010), here that suggestion is much stronger because other possible factors (e.g., rainfall, climate, temperature) are very similar among the plots. There were very few species and genera in common among the three forests and so soils seem to associate with, and perhaps help to cause, their own unique flora. Among the taxa, there was more similarity on the familial taxonomic level consistent with the hypothesis that a small number of plant families dominate in the Neotropic (Oligarchies: Honorio-Corondo, 2009). The edaphic conditions found in white sand forest and palm forest reduced tree stem density to a degree, and palm forest had smaller stems than the other two forest-types. White sand forest had a reduction to 1/3 of the species richness of *terra firme* and palm forest was half that of white sand forest. Basal areas were similar in white sand forest and palm forest, but both were less than *terra firme.* White sand forest had more above-ground biomass than *terra firme* forest. Soils with reduced nutrients (white sand forest) and those that were waterlogged (palm forest) were found with more open canopies compared to *terra firme* forest.

Pittman *et al*. (2008) sampled plots the same size, shape, and lower stem size limit as this study, and found a major floristic discontinuity between *terra firme* and white sand forest in the western Amazon, thought to depend on soil characteristics (Fine *et al.*, 2007; Vormisto *et al.*, 2000). Fine *et al.* (2010) sampled mainly 0.1 ha white sand plots at a minimum stem size of 5 cm dbh and found a species richness of 41.5 on average which was smaller than *terra firme* forests, and a different species composition than *terra firme* forest (as seen here) with 83% endemics found only in white sand forest and dominance by a relatively few species. The species found in those plots, were very similar to mine, but in smaller white sand plots (Fine *et al*., 2010). The low soil nutrients in white sand forest may have been the cause of the reduction in stem density and species richness, compared to *terra firme* forests, but did not affect the size structure of those stems.

In addition to the comparisons of white sand forest, palm forest and *terra firme* forest made here, it is useful to also compare the results to one ha plots (again all trees with a dbh at least 10 cm) sampled in white-water flooded forest in Ecuador (várzea: flooded 1 month per year) and sampled in black-water flooded forest in Peru (igapó: flooded 3-4 months per year) where I computed the same structural parameters (Myster, 2015; Myster, 2016a; Myster, 2016b). Floristic similarity is still low between white sand and these two flooded forests at genus and species levels. The number of families in white sand (15) different from várzea (at 41) but similar to igapó (at 16). But there are few families they have in common (4 white sand families out of 16 in igapó, 12 white sand families out of 41 in várzea). Rankings of the common families are also different. For example, whereas Fabaceae is easily the most common family in both flooded forests, it ranks only ninth in the white sand forest, and where Cluciaceae is the most common in the white sand forest, it ranks 21st in the várzea forest and is not found in igapó. This floristic comparison suggests that white sand may become similar to igapó forest in number of families when flooded is at least 4 months per year. *Terra firme* and várzea were similar in families while palm remained largely unique.

In terms of stand structure, the white sand forest (403 stems/ha) is closer to várzea (573 stems/ha) than to igapó (167 stems/ha). There were more, large trees in both flooded forests, however, and more species in both várzea (185 species/ha) and igapó (120 species/ha) compared to 103 species in the one ha white sand plot. White sand basal area and aboveground biomass was between the two flooded forests due to the increased number of stems, but várzea was more closed (44.7 %) than either white sand (14.4 %) or igapó (12.3 %). Several structural parameters continue to suggest that white sand may be similar in structure (and some families) to igapó forests that are flooded more than 4 months per year (Myster, 2007; Myster, 2010; Myster, 2015; Myster, 2016a; Myster, 2016b). Compared to *terra firme* forests both white sand forest and flooded forests lose stems, but flooded forests maintain a greater number of larger trees than both unflooded forests – white sand, *terra firme* – and so their stem distribution is more of a "saddle" than a monotonic decline in numbers with increasing size (Myster, 2016b). As flooding increased, there was increased basal area and fewer trees, genera, and species (Myster, 2010). Both reduced soil nutrients and flooding tend to eliminate both vertical and horizontal heterogeneity affecting, for example, the availability of commonly logged tree species and animal populations. The white sand plot suggests that loss of soil fertility may have similar effects on certain forest structural parameters as flooding, for some black-water forests at least.

Species identity in the palm study plot compared well with other palm forest samplings in the western Amazon (Svenning, 1999a; Vormisto *et al.,* 2000, Montufar and Pintaud, 2006; Normand *et al.,* 2006) but structural analysis in palm forests has not been done before and so data was not available for comparison. The reduction in species richness for palm forests, compared to other *terra firme* forests, has also been predicted (Normand *et al.,* 2006). Sitting water in palm forest leads to less stems and smaller stems compared to *terra firme* forest as does flooding**,** but flooded forests maintain a greater number of larger trees and so their stem distribution is more of a "saddle" than a monotonic decline in numbers with increasing size (Myster, 2016b). This is seen in the increased basal area and leading to fewer trees, genera, and species as flooding increased (Myster, 2007; Myster, 2010). Both standing water and flooding tend to eliminate both vertical and horizontal heterogeneity affecting, for example, the availability of commonly logged tree species and animal populations. Results suggest that loss of soil fertility and standing water in unflooded forests may have similar effects on certain forest structural parameters as flooding of both white-water and black-water.

Finally, tree seed studies have shown that in *terra firme* forest seed predators took most seeds regardless of species, in palm forest species were different regardless of seed mechanism and tolerance, and in white sand forest seed predators took most seeds regardless of species. That is while seed predation losses strength as forests become more stressed by loss of soil fertility, seed pathogens become more important with water-logged soils (Myster, 2017b). These permanent plot studies, and others like them in the Amazon, provide baseline data on forest dynamics and fluctuations of forest structure which are due to plant-plant replacement (Myster, 2012; Myster, 2017a). 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.

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