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RESEARCH ARTICLE

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Floristics and physical structure of five Amazon plots in Ecuador and Peru

Randall W. Myster [1]*

[1]Randall W. Myster,Biology Department,
Oklahoma State University, Oklahoma City,
OK, USA

Correspondence
Randall W. Myster,Biology Department,
Oklahoma State University, Oklahoma City,
OK, USA
Email: mysterrwm1@gmail.com

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ABSTRACT

The Amazon contains some of the most important forested ecosystems on earth and so we need to know the nature and degree of their similarities and differences. Therefore I compared the floristics and physical structure of five common Amazonian forest-types (terra firme, palm and white sand [all unflooded], várzea and igapó [both flooded]) with data from separate one ha plots in the Ecuadorean and Peruvian Amazon. I found (1) the most abundant families were Arecaceae, Fabaceae, and Clusiaceae and those families along with Euphorbiaceae were the only families found in all five plots, (2) the highest stem density, the greatest number of large stems and the most closed canopy were in várzea and terra firme, (3) palm had the most median stems and the smallest average stem size, and (4) igapó had the smallest basal area and above-ground biomass. Ordination on the five plots then suggested that Arecaceae and Clusiaceae best defined the floristic data, and total stems and smallest stem size class best defined the physical structure data. Cluster analysis after ordination (1) based on floristics, showed that terra firme, várzea and igapó formed a cluster and both palm and white sand were in separate clusters by themselves, and (2) based on physical structure, showed that terra firme and palm formed a cluster, white sand and igapó formed a cluster and várzea was in a cluster by itself. While results suggest that soil characteristics are important in determining the floristic composition of Amazon forests and flooding characteristics are important in determining their physical structure, they can only set-up hypotheses to test by future sampling of these forest-types elsewhere in the Amazon.

KEYWORDS
Igapó, palm, terra firme, várzea, white sand

INTRODUCTION

Across Amazonia are some of the most important forested ecosystems on earth due to their (1) high biodiversity, (2) significant influence on the water cycle, the oxygen cycle, the carbon cycle and other global biogeochemical cycles, and (3) ef-

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fect on the world's climate (Myster, 2009), and so understanding them is critical in helping us prepare for our shared human future. Among the most common unflooded forest-types in the Amazon are terra firme found on fertile clay or loam soils (Daly & Prance, 1989), palm found on moderately fertile soils that are permanently waterlogged, and white sand found on infertile soils made up mainly of quartz podzols (Tuomisto *et al.*, 2003; Honorio, 2006; Myster, 2017a, 2018a).

Moreover terra firme has the most species and complex structure, white sand has the least species and relatively simplest structure, e.g., dominated by only a few tree species but high in endemic species (Fine *et al.*, 2010); and palm which has a species richness and structure between terra firme and white sand (Vormisto *et al.*, 2004; Myster, 2017b). Among the most common flooded forest-types in the Amazon are várzea flooded by white-water (run-off from the Andean mountains) and igapó flooded by black-water leached from local forest litter Myster (2018b, 2019); Junk *et al.* (1989).

That white-water has high amounts of suspended matter and concentrations of phosphorus (P) and potassium (K), and the black-water has low amounts of suspended matter and concentrations of P and K, but high amounts of humic acid. These five common Amazonian forest-types – terra firme, palm, white sand, várzea, and igapó – share several key characteristics (e.g., in floristics and physical structure) with other forest-types found throughout the rest of the Neotropics (Kalliola *et al.*, 1991; Pitman *et al.*, 2001; Tuomisto *et al.*, 2003) and so the results of this study may have wider utility.

Here I investigate the five common Amazonian forest-types by first complying, comparing and contrasting the tropical plant families sampled in their separate one ha plots, then computing, comparing, and contrasting key structural parameters for each of the five forest-types using data sampled in the same one ha plots (Wilson, 1991; Pitman *et al.*, 2008; Fine *et al.*, 2010) and finally combining the data from all five one ha plots together and using it in ordination and clustering procedures to determine which families and structural parameters are important in defining the plots (and by implication the forest-types they were sampled in), how those plots (forest-types) separate and cluster along generated ordination axes, and whether or not any hypotheses can be drawn from these ordination and clustering patterns.

METHODS

Study sites.- The first study site was the Sabalillo Forest Reserve (SFR: 3º 20' S, 72º 18' W) established in 2000 and operated by Project Amazonas (www.projectamazonas.org: Moreau, 2008). The reserve is located on both sides of the upper Rio Apayacuo and is 172 km east of Iquitos, Peru. SFR is part of 25,000 hectares set aside over the last decade and is comprised of low, seasonally inundated river basins of the upper Amazon. Annual precipitation is 3297 mm per year and the rainy season is between November and April (Choo *et al.*, 2002). Within the reserve, black-water runoff creates igapó forests, with terra firme forest, white sand forest, and palm forest common as well. The second study site was the Estación Científica Yasuní (ECY: 0º 41' S, 76º 24' W), operated by the Pontificia Universidad Catolica of Ecuador (www.puce.edu.ec) and located within the Yasuni National Park of eastern Ecuador (Duivenvoorden *et al.*, 2001). ECY mean annual rainfall is 3081 mm and the station is wettest between the months of April to May and October to November. August is the driest month and the mean monthly temperature varies between 22º C and 35º C. Soils in the National Park are clayey (i.e., low in most cations but rich in aluminum and iron: Tuomisto et al., 2003). Although most of the station is terra firme forest, várzea forest – located next to the white-water Tiputini River and underwater between the months of October and April for a few weeks to a maximum depth of 3 m – is also common. ECY is also the site of a long-term 50 ha vegetation plot in terra firme forest, maintained by the Pontificia Universidad Católica del Ecuador as part of ForestGEO network.

The third study site was the Área de Conservación Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: 4º 18' S, 73º 13' W) located in Loreto Province, 130km south of Iquitos, Peru (www.perujungle.com: Gottdenker & Bodmer 1998). It is part of one of the largest (270,654 ha) protected areas in the Amazon, containing wet lowland tropical rainforest of high diversity (Daly & Prance, 1989). ACRCTT is comprised of low, seasonally inundated river basins of the upper Amazon and named for two of the major white-water rivers – the Tamshiyacu and the Tahuayo – that form boundaries to the north and west. Annual precipitation ranges from 2400 – 3000 mm per year, and the average temperature is relatively constant at 26º C.

Plot set-up and sampling.- My field assistants and I set-up and sampled all trees and palms at least 10 cm diameter at breast height (dbh) in a one ha plot (200 m x 50 m) in várzea (under water 1 month per year) at ECY in May 2010. We also set-up and sampled a one ha plot in igapó (under water 2 months per year) at ACRCTT in May 2011 and one ha plots in terra firme, palm, and white sand at SFR in June 2013. All plots were the same shape, and sampled using the same sampling protocols that included that all dbh measurements be taken at the nearest/lowest point when the stem was cylindrical, and just above the buttresses when the tree was buttressed. Trees were identified to species or, in a few cases, to genus only using Romoleroux *et al.* (1997) and (Gentry, 1996) as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana (UNAP) herbarium in Iquitos and the Missouri Botanical Garden website www.missouribotanicalgarden.org. Voucher samples are kept at the ECY or UNAP herbaria. The plot data from várzea and igapó are archived at the Luquillo Experimental Forest in Puerto Rico as LTERDBAS#172 which is part of the Long-term Ecological Research program funded by the US National Science Foundation https://lternet.edu/.

Data analyses.- For each one ha plot, the number of tree stems in each family was first complied. The number of tree stems per species was also generated but not used for further analysis because it generated a matrix with too many zeroes (a very sparse matrix: Pielou, 1991; Ludwig & Reynolds 1988). Then for each one ha plot, these structural parameters were computed: (1) the total number of tree stems, the total number of tree stems divided into these four size classes: 10-19 dbh, 20-29 dbh, 30-39 dbh and ≥40 dbh, and mean dbh, (2) tree species richness, (3) the sum of the basal areas of all individual tree stems ($\sum \pi r^2$; where r = the dbh of the individual stem / 2), (4) above-ground biomass using the formula in Nascimento & Laurance (2002) suggested for tropical 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 one ha plot area closed. The family and physical structure data from each of the five separate plots has been published previously (Myster, 2013, 2015, 2016a,c,b, 2018a,b,c). Finally a principal components analysis using a correlation matrix (PCA: Ludwig & Reynolds, 1988; Pielou, 1991; Myster, 2012a) was performed on both the familial data (using a forest-types x plant families matrix derived from Table 1) and on the physical structure data (using a forest-types x structural parameters matrix derived from Table 2). To examine any possible distortion of the data by PCA (e.g., a horseshoe effect: Minchin, 1987; Legendre & Gallagher, 2001), I also performed a non-metric multidimensional scaling ordination (NMDS: Myster & Malahy, 2008) on the same two matrices. If there was no distortion, a cluster analysis employing single-linkage clustering without normalization (SAS, 1985; P. Morin pers., comm.) was performed using the axis coordinates generated by PCA for each of the five forest-types.

RESULTS

I found 58 plant families among the five one ha plots and 19 families in only one plot (11 of those families were unique to terra firme: Table 1). The families with the most stems were Arecaceae (305 stems), Fabaceae (283 stems) and Clusiaceae (240 stems: Table 1) and those three families along with Euphorbiaceae were the only families present in all five plots. The three most abundance tree species in each forest-type (listed in decreasing order of abundance) were: in terra firme forest *Astrocaryum murumura*, *Otoba parivifolia* and *Iriartea deltoidea*, in palm forest *Socratea exprrhiza*, *Lepidocaryum tenue* and *Oenocarpus bataua*, in white sand forest *Pachira brevipes*, *Caraipa tereticaulis* and *Tovomita calphyllophylla*, in várzea forest *Inga spectabilis*, *Macrolobium acasifolium* and *Inga leiocalycina* and in igapó forest *Aldina latifolia*, *Caraipa grandifolia* and *Virola elongate*. I found the greatest stem density, the greatest number of large stems and the most closed canopy in várzea forest and in terra firme forest (Table 2). Species richness was much greater in terra firme compared to all other forests. Whereas palm forest had the most medium-sized stems and the smallest mean dbh, igapó forest had the smallest basal area and above-ground biomass (Table 2).

The PCA using data derived from Table 1 differentiated well among the plots with the first PCA axis explaining 54.2% of the original variation and the second PCA axis explaining 22.1%. The families most important in defining the first PCA axis were Arecaceae (Pearson's product-moment correlation coefficient [PPMCC] = 4.23, p = 0.021) and Clusiaceae (PPMCC= 3.11, p = 0.024). The most common species in those families were *Astrocaryum murumura*, *Euterpe precatoria*,

TABLE 1 All families found in the five 1 ha plots sorted alphabetically with the number of tree stems sampled given under each forest type.

Family	Terra firme	Palm	White sand	Várzea	Igapó
Anacardiaceae	4	0	0	1	0
Annonaceae	36	0	11	15	0
Apocynaceae	1	0	0	3	3
Araliaceae	2	0	0	0	0
Arecaceae	30	235	1	21	18
Begoniaceae	1	0	0	1	0
Buxaceae	0	0	0	18	0
Bombacaceae	50	0	0	27	0
Boraginaceae	4	0	0	0	0
Burseraceae	18	0	23	5	0
Calophyllaceae	0	0	0	0	8
Capparaceae	1	0	0	0	0
Caricaceae	3	0	0	0	0
Cecropiaceae	5	0	0	44	0
Chrysobalanaceae	9	0	0	10	5
Clusiaceae	1	98	127	7	7
Combretaceae	0	0	0	1	0
Dichapetalaceae	1	0	0	1	0
Ehretiaceae	0	0	0	1	0
Elaeocarpaceae	1	0	3	2	0
Euphorbiaceae	18	8	3	36	8
Fabaceae	55	57	7	125	39
Humiriaceae	0	15	0	0	0
Icacinaceae	1	0	5	1	0
Lauraceae	19	0	0	8	5
Lecythidaceae	18	36	0	31	13
Malpighiaceae	1	0	0	0	4
Malvaceae	0	0	86	0	4
Melastomataceae	1	0	0	20	9
Meliaceae	22	0	0	45	1
Memecylaceae	1	0	0	0	0
Moraceae	22	0	1	23	11
Myristicaceae	56	0	0	12	8
Myrtaceae	6	0	64	1	0
Nyctaginaceae	9	0	0	15	0
Ochnaceae	0	0	0	1	0
Oleaceae	1	0	0	2	0
Opiliaceae	0	1	0	0	0
Picramniaceae	0	0	0	2	0

Polygonaceae	4	0	0	4	0
Quiinaceae	1	0	0	0	0
Rhizophoraceae	1	0	0	0	0
Rubiaceae	4	0	48	10	12
Sabiaceae	1	0	0	2	0
Salicaceae	7	0	0	15	2
Sapindaceae	2	0	10	11	0
Sapotaceae	42	0	3	14	5
Simaroubaceae	1	0	0	3	0
Siparunaceae	4	0	9	0	0
Staphyleaceae	1	0	0	0	0
Sterculiaceae	17	0	0	4	0
Tiliaceae	8	0	0	0	0
Ulmaceae	6	0	0	1	0
Urticaceae	3	0	0	0	0
Verbenaceae	1	0	0	0	0
Violaceae	4	0	2	0	0
Vochysiaceae	0	0	16	0	5

Geonoma macrostachys, *Iriartea deltoidea* and *Oenocarpus batana* (all in Arecacae), and *Caraipa valioi*, *Caraipa tereticaulis*, *Calophyllum brasiliense* and *Tovomita macrophylla* (all in Clusiaceae). The families most important in defining the second PCA axis were Malvaceae (PPMCC = 2.23, p = 0.033) and Myrtaceae (PPMCC= 1.91, p = 0.039). The most common species in those families were *Pachiva brevipes* and *Theobroma cacao* (both in Malvaceae), and *Marlierea caudate* (in Myrtaceae). NMDS showed no distortions in the PCA so I used the PCA axis coordinates of each forest-type for the cluster analysis, which generated these three clusters: terra firme, várzea and igapó in one cluster, palm in one cluster, and white sand in one cluster.

The PCA using data from Table 2 also differentiated well among the plots with the first PCA axis explaining 44.3% of the original variation and the second PCA axis explaining 20.9%. The parameters most important in defining the first PCA axis were total stems (PPMCC = 3.93, p = 0.022) and smallest stem size class (PPMCC= 3.01, p = 0.025), and the parameters most important in defining the second PCA axis were the next smallest stem size class (PPMCC = 2.87, p = 0.028) and species richness (PPMCC= 2.51, p = 0.027). NMDS again showed no distortions in the PCA so I used the PCA axis coordinates of each forest-type for the cluster analysis, which generated these three clusters: terra firme and palm in one cluster, white sand and igapó in one cluster, and várzea in one cluster.

DISCUSSION

Although there were common families among the five plots there were more families with only one stem found among the plots. Clustering based on familial floristics showed white sand forest and palm forest were most different, and terra firme forest, várzea forest and igapó forest were most similar. Possible explanations for this clustering pattern include (1) species migrating from terra firme into the flooded forests and forming ecotypes (Wittmann *et al.*, 2010), (2) flooded forests that are actually terra firme forests that lost species when they flooded, or (3) palm and white sand forests species existing in unique, harsh environments of either long periods of water-logged soil (palm) or low nutrient availability (white sand). These results suggest a hypothesis (to test in future sampling) that soil differences among these forest-types may be affecting floristics more than flooding differences. Clustering results also suggest this strategy for management and restoration of the five study forest-types: use tree species successful in one forest-type to manage/restore the floristics of other forest-types if they are in the same cluster.

TABLE 2 Forest community structural parameters for all trees at least 10 cm dbh sampled in all five 1 ha plots (Myster, 2013; Myster, 2015; Myster, 2016a; Myster, 2016b; Myster, 2016c; Myster, 2018a; Myster, 2018b; Myster, 2019). All data are per hectare, regardless of how they were sampled.

Parameter	Terra firme	Palm	White sand	Várzea	Igapó
Stem density:					
Total:	519	449	403	573	167
[10, 20) dbh	288	253	241	366	84
[20, 30) dbh	121	176	95	87	58
[30, 40) dbh	50	20	63	39	17
≥40 dbh	60	0	3	81	8
mean dbh	20.8	14.1	19.8	24.2	22.3
Species richness	302	57	103	159	31
Basal area (m^2)	17.6	11.15	12.52	26.3	6.52
Above-ground biomass (Mg)	334.2	267.1	187.7	292	202
Canopy closure (m^2)	6921.4	2356.7	1441.2	4478.04	1231.22
Canopy closure per ha (%)	69.214	23.567	14.412	44.7804	12.3122

Terra firme plots in the Peruvian Amazon had more stems, larger stems and more basal area and above-ground biomass than flooded plots. Indeed compared to terra firme both white sand and igapó lose stems, but várzea maintains a greater number and percentage of larger trees than all unflooded forests. And so, várzea stem distribution is more of a “saddle” than a monotonic decline in numbers with increasing size. There was a general increase in basal area, with fewer trees, genera, and species, as flooding increased. Sampled data for basal area, stem density and species were consistent with larger scale sampling across the Amazon (Malhi *et al.*, 2002; Peacock *et al.*, 2007; Stropp *et al.*, 2009). Clustering based on structural parameters showed that várzea forest is most different, and that the two forests under the most stress – igapó forest (from nutrient-poor water) and white sand forest (from nutrient-poor soil) – are most similar, suggesting another hypothesis (to test in future sampling) that while difference in flooding characteristics have a different effect on structure, difference in kinds of stress have a similar effect on structure. Clustering results also suggest this strategy for management and restoration of the five study forest-types: use tree species successful in one forest-type to manage/restore the physical structure of other forest-types if they are in the same cluster.

Mechanisms affecting tree seeds and seedlings are very important to the floristics and physical structure of these forested ecosystems (Myster, 2009). And so I have conducted several field experiments in these forest-types including for seeds (1) I found terra firme lost most of their seed to predators and the least of their seed to pathogens, white sand forests lost the least of their seed to predators and the most of their seed to pathogens, and the fewest seeds germinated in both terra firme forests and in palm forest, within unlogged terra firme forest addition of litter reduced seed predation but increased seed losses to pathogens and germination, and C.latiloba lost the most seeds to pathogens, within palm forest addition of litter reduced predation but increased losses to pathogens, and S.exorrhiza lost the least seeds to pathogens, and within white sand forests addition of litter increased germination (Myster, 2021), and for seedlings (2) Ecuadorean Amazon terra firme forest which showed that tree seedlings were stressed more by lack of water (drought) than by lack of sunlight (shading: Myster, 2012) suggesting that competition for water is more critical than competition for light for seedlings in terra firme forests of the Amazon.

Seedlings of all tree species and in all forest-types also suffer from the stress of intense herbivory (Myster & McCarthy, 1989) due to Amazonian animals (Myster, 2017b, 2018b,c, 2016c,b). And in the flooded forests of várzea and igapó tree species that succeed as seeds and seedlings must have strong adaptations that reduce the stress of flooding (Myster, 2018b). These adaptations include seeds that disperse and germinate quickly when flood waters recede (to avoid seed predators and pathogens: Myster, 2009; Myster, 2018b) and seedlings that grow fast in order to survive when flooding returns.

Soil characteristics may affect floristic differences between terra firme and white sand forest (Pitman *et al.*, 2008) and other samplings done in forests across the Amazonian landscape (Umana *et al.*, 2010) suggest that while soil fertility affects floristics, flooding reduces physical structure such as species richness and canopy-closure. With the samplings done in this study, however, it is difficult to tease apart these differences without more sampling, compilation and computation within these Amazon forest-types. That is to say that there may be other mechanisms and methodologies that affect family composition and physical structure in these forests that warrant further study – such as broad-scale biogeographic and evolutionary processes, as well as habitat specialization (Fine & Kembel, 2011; Myster, 2012b) and the effects of flooding frequency and sedimentation – and only when we examine them through more sampling may we be able to discover the causes of Amazon forest composition and structure, and thus be better able to manage and restore them.

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CONFLICTS OF INTEREST

The author declare no conflicts of interest.

RESUMEN

Florística y estructura física de cinco parcelas amazónicas en Ecuador y Perú.

El Amazonas contiene algunos de los ecosistemas boscosos más importantes de la tierra, por lo que necesitamos conocer la naturaleza y el grado de sus similitudes y diferencias. Por lo tanto, comparé la estructura florística y física de cinco tipos de bosques amazónicos comunes (tierra firme, palma y arena blanca [todos sin inundación], várzea e igapó [ambos inundados]) dentro de parcelas separadas de una hectárea en la Amazonía ecuatoriana y peruana. Encontré que (1) las familias más abundantes eran Arecaceae, Fabaceae y Clusiaceae y esas familias junto con Euphorbiaceae fueron las únicas familias encontradas en las cinco parcelas, (2) la mayor densidad de tallos, el mayor número de tallos grandes y los más cerrados el dosel estaba en várzea y tierra firme, (3) la palma tenía los tallos más medianos y el tamaño promedio de tallo más pequeño, y (4) igapó tenía el área basal y la biomasa aérea más pequeñas. La ordenación sugirió que Arecaceae y Clusiaceae definieron mejor los datos florísticos, y los tallos totales y la clase de tamaño de tallo más pequeño definieron mejor los datos de estructura física. El análisis de conglomerados después de la ordenación (1) basado en florística, mostró que tierra firme, várzea e igapó formaron un racimo y tanto la palma como la arena blanca estaban en racimos separados por sí mismos, y (2) según la estructura física, mostró que la tierra firme y la palma formó un racimo, arena blanca e igapó formó un racimo y várzea estaba en un racimo por sí mismo. Si bien los resultados sugieren que las características del suelo son importantes para determinar la composición florística de los bosques amazónicos y las características de las inundaciones son importantes para determinar su estructura física, solo establecen hipótesis para ser probadas mediante muestreos futuros de estos tipos de bosques en otras partes del Amazonas.

PALABRAS CLAVE: Igapó, palma, tierra firme, várzea, arena blanca.

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