

1 **EDAPHIC FACTORS AND FLOODING PERIODICITY DETERMINING**  
2 **FOREST TYPES IN A TOPOGRAPHIC GRADIENT IN THE NORTHERN**  
3 **BRAZILIAN AMAZONIA**

4  
5  
6 **Abstract**  
7

8 The Brazilian Amazonia is a region covered by an extensive mosaic of tropical forests  
9 conditioned by different topographical and hydro-edaphic features. Although studies  
10 relating environmental determinants of structure and floristic composition are  
11 systematically evolving in the region, there is no doubt that there are still information  
12 gaps due to the lack of research in peripheric areas of the Amazonia. The seasonally  
13 flooded areas of the state of Roraima situated on rio Branco-rio Negro basin, northern  
14 Brazilian Amazonia, still are deprived of such information. In this way, this work had as  
15 objective determine the physical and soil chemical attributes, and the flooding  
16 periodicity that characterize different forest types dispersed in a topographic gradient  
17 located in an area on the north of rio Branco-rio Negro basin. Soil samples (0-60 cm)  
18 were collected along a 2.7 km transect (31.1-64.8 m a.s.l.) crossing three different forest  
19 types: (i) mosaic between treed and forested shade-loving (La+Ld), (ii) area of  
20 ecological tension between forested shade-loving and open ombrophilous forest (LO)  
21 and (iii) open ombrophilous forest (Ab+As). The results indicated different soil classes  
22 and flooding periodicity for each forest type observed: Entisols Fluvents (La+Ld, 3-4  
23 months flooded), Entisols Quartzipsamments (LO, 1-2 months) and Yellow Ultisols  
24 (Ab+As, no flooding). All analyzed soils were defined as nutrient-poor areas, especially  
25 those located on low altitude, characterized for higher hydrological restrictions  
26 (seasonal flooding) aggregating forest types of lower structural patterns (e.g. La+Ld).  
27 Soils on low altitude were also characterized as those with the highest percentage of fine  
28 sand and silt, while soil free of seasonal flooding (Yellow Ultisols) presented the  
29 highest levels of clay and coarse sand, always associated with the ombrophilous forests  
30 (higher structural patterns). These results improve our understanding of the  
31 environmental factors conditioning different forest types in this peripheral region of  
32 Amazonia, suggesting that ecosystems with higher hydro-edaphic restrictions are a  
33 strong indicator of forest types with lower structural patterns.

34 Keywords: oligotrophic ecosystems, water table, ecotone, phytophysiognomy.  
35

36 **INTRODUCTION**

37 The Amazon basin occupies ~40% of the surface of South America and about 60%  
38 is inserted within the Brazilian territory [1]. Its predominant covering is defined as  
39 dense and open ombrophilous forests [2-3], but throughout the Amazonian biome there  
40 are many different forest types that may be distinguished by their floristic composition  
41 and structure due to the large environmental heterogeneity [4-5]. In general, the factors  
42 modeling the different forest types are attributed mainly to the climatic variations,  
43 hydro-edaphic conditions, topography, and anthropogenic interferences, all interacting

44 and acting at different spatial scales [6-9]. This congregation of factors generates  
45 different structural and floristic shades with different ecosystem values, but generally  
46 information on the weight of each one, in the local and regional context, is little known  
47 due to the gigantism of the Amazonia, which makes sampling in peripheral areas a  
48 difficult process [3,10]. However, this kind of information is the basis for improving our  
49 knowledge on specialization of the various Amazonian phytophysiognomies, with  
50 different structural patterns and species diversity, directly influencing the estimates of  
51 biomass/carbon stocks and fluxes in this region considered to be the largest and most  
52 important "natural environment" mitigating the harmful effects of global climate change  
53 [11-12].

54 Although studies involving edaphic and hydrological factors in association with  
55 topographic gradients related to the dynamics of ecosystems have evolved rapidly in the  
56 Amazon [14-16], there is still a great lack of information due to huge regional gaps with  
57 rare scientific investigations. In this context, ecotone forests (transition areas, contact  
58 zones or areas of ecological tension) are ecoregions representing about 15% of the  
59 biome [17] but still have a lack of knowledge about the processes of their formation and  
60 maintenance [18]. These ecoregions are characterized by mosaics of different forest  
61 types condensed into distinct spatial scales that hamper their floristic and structural  
62 characterization and, above all, biomass/carbon estimates [19, 20]. This scarcity is  
63 mainly detected in the northern of the Brazilian Amazonia, especially in the seasonally  
64 flooded areas of the rio Branco-rio Negro basin located in the state of Roraima [16, 21-  
65 22].

66 Recent works have demonstrated that the ecosystems which form the mosaic of  
67 landscapes in this region present a direct integration between the plant cover and the  
68 physical, chemical and biological attributes of the soil [23] due to essential processes  
69 related to the biogeochemical cycles, water table outcrops, accumulation and  
70 decomposition of organic matter [16, 24]. This is a strong indication that environmental  
71 conditions associated with temporal flooding, sediment drag, and nutrient leaching may  
72 have high importance in the formatting of different forest types in this peripheral region  
73 of the Amazonia [25-27]. In the same context, the physical and chemical attributes of  
74 the soil, altitude, flooding periodicity, drainage and microclimate also considered as  
75 important determinants in the formation of different natural environments with specific  
76 structural patterns [28-29].

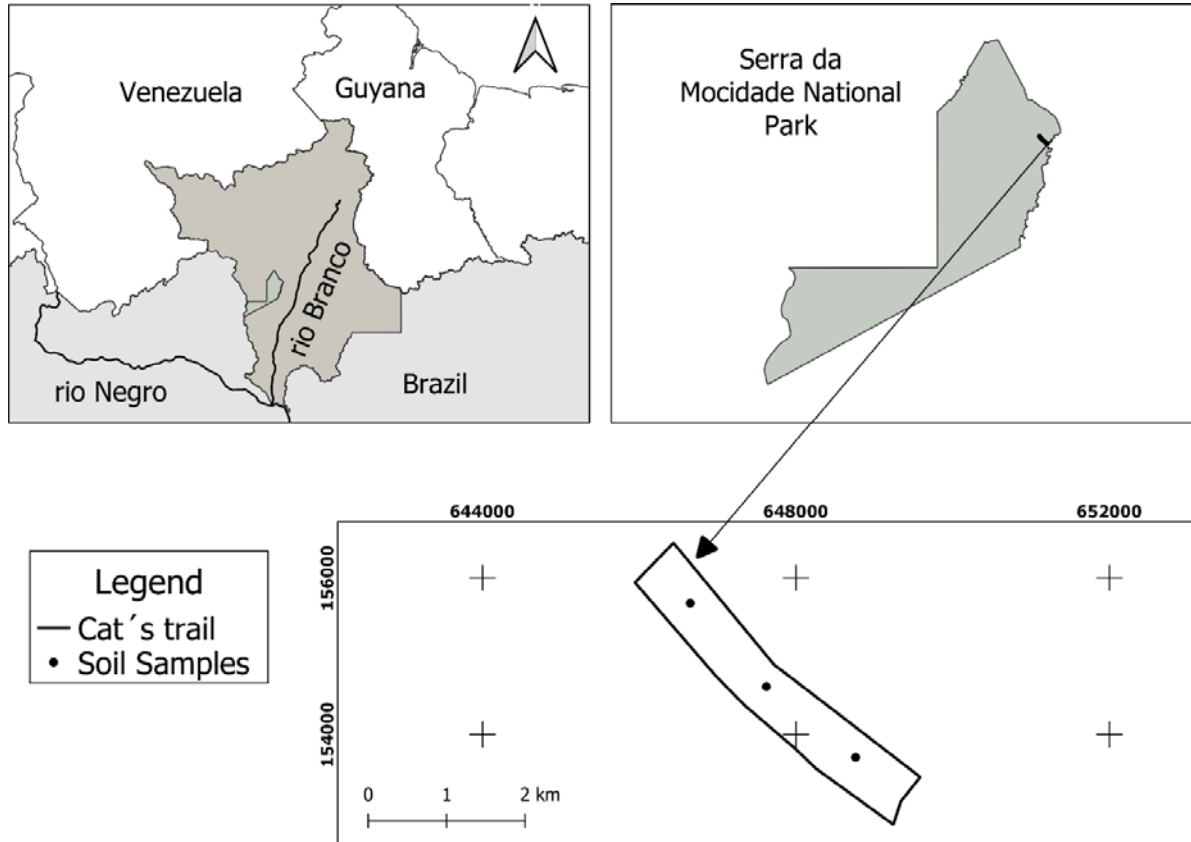
77 The objective of this study was to determine the flooding periodicity and the  
78 physical and soil chemical attributes that characterize a topographic gradient established  
79 between the Água Boa do Univini River and the Cumaru Mountain, a peripheral area of  
80 the Rio Branco-Rio Negro basin. This region belongs to the Serra da Mocidade National  
81 Park, a federal protected area located in the state of Roraima, northern Brazilian  
82 Amazonia. This region is formed by a large mosaic of forest and non-forest ecosystems  
83 without rare scientific investigations about the role of hydro-edaphic factors as  
84 determinants of different phytophysiological formations. Our results aim to improve  
85 the understanding of the environmental factors that determine different forest types in  
86 this region of Amazonia, indicating the association between environments with  
87 higher/lower hydro-edaphic restrictions and their respective forest structural pattern  
88 taking into account horizontal (stem diameter) and vertical (total height) parameters.

## 89 **MATERIALS AND METHODS**

### 90 **Study area**

91 This study was carried out in the Serra da Mocidade National Park (1.405° N -  
92 61.648° W and 1.382° N - 61.673° W), a federal protected area managed by ICMBio  
93 (Chico Mendes Institute for Biodiversity and Conservation), located in the municipality  
94 of Caracarái, ~ 290 km south of Boa Vista, capital of Roraima. The sampling area is  
95 characterized by ecotone zones (area of ecological tension or transition area or contact  
96 zone) between seasonally flooded forests under strong influence of the Água Nova do  
97 Univini river (black water) in association with open ombrophilous forests that reach the  
98 first steps of elevation of the Cumaru Mountain (Figure 1). The phytophysiological  
99 characterization, edaphic and flood periodicity were performed in a topographic  
100 gradient (31.1-64.8 m a.s.l.) inserted in an irregular transect (2.7 km long) known as  
101 "Cat's Trail", which begins on the right bank of the Água Boa do Univini river to the  
102 first steps of the northeast sector of the Cumaru Mountain, located at the northeastern  
103 end of the National Park (Figure 1).

104 **Figure 1** - Study area indicating the geographical location of the Serra da Mocidade  
105 National Park and the soil profiles sampled along the Cat's Trail.



106

### 107 **Characterization of the study area**

108 The National Park is totally inserted in the rainy tropical monsoon type (Am)  
109 following Köppen classification, with annual rainfall of 1700-2000 mm and May-  
110 August representing the rainiest period (~40% of annual rainfall [30-31]. This region is  
111 marked by a chain of mountains that lends its name (Serra da Mocidade), resulting from  
112 the erosion of the Guyanese Craton, a large continental block formed by magmatic and  
113 metamorphic rocks dated between 1.8-2.5 billion years, in the Lower Pre-Cambrian  
114 period [32]. The characteristics of the main soil types in the National Park region are  
115 defined from lithological residues of the same geological constitution of the rock  
116 formation complex of the Serra da Mocidade, being a large residual mass, with an  
117 altitude reaching ~1.800 m, characterized by sharp crests and ravine slopes, covered by  
118 high altitude forests that lose this characteristic when reaching the zones of flooded  
119 forests of low altitude and smaller biometric structural patterns. Along this rocky  
120 complex, eight different soil classes can be found: Neossolo Flúvico (Entisols Fluvents),

121 Neossolo Quartzarênico (Entisols Quartzipsamments), Espodossolo Humilúvico  
122 (Spodosols), Latossolo Amarelo (Yellow Oxisols), Gleissolo Háptico (Entsols),  
123 Latossolo Vermelho (Red Oxisols), Neossolo Litólico (Entsols Lithic) and Argissolo  
124 Amarelo (Yellow Ultisols) [32-33].

### 125 **Phyto-characterization and periodicity of flooding**

126 In order to carry out the phytophysionomic classification of the forest types in  
127 the sample area, we adopted the criteria proposed by the Brazilian Vegetation  
128 Classification System [34], based on a forest inventory carried out along the entire  
129 transect at Cat's Trail (R. I. Barbosa, personal communication). In this survey, the  
130 structure (horizontal and vertical) and arboreal groups (trees and palms) with stem  
131 diameter  $\geq 10$  cm were defined in each forest type arranged along the topographic  
132 gradient (31,1-64, 8 m a.s.l.). The flood periodicity data were obtained from  
133 observations performed in two consecutive rainy periods (2016 and 2017), where the  
134 sampling transect was coursed from start to finish in both periods, estimating a mean  
135 time interval (months) of flooding for each of them. All information was aggregated  
136 into an ecosystem conceptual model that faithfully followed the observed topographic  
137 gradient. Later, this model was adopted as an associative basis of the chemical and soil  
138 physical characteristics under each defined forest type.

### 139 **Soil sampling and physical/chemical analyzes**

140 In order to analyze and describe the physical and chemical attributes of the soil,  
141 three profiles (1m wide, 1m long, 80cm deep) were opened for each forest type  
142 considered. Soil samples were collected at 0-20cm, 20-40cm and 40-60cm depths. After  
143 that, the samples were deposited in plastic bags and identified by forest type and depth.  
144 All samples were air dried (TFSA), sieved (2 mm) and sent to the Soil Laboratory for  
145 physical (% sand,% silt and% clay) and chemical (pH, organic matter, exchangeable  
146 acidity, potential acidity, Ca, Mg, K, P, Cu, Zn, Fe, Mn and B) analysis following the  
147 methodology specified [35]. The descriptive classification of the soils sampled was  
148 performed by the Brazilian Soil Classification System [36] up to the third categorical  
149 level and correlated to the Soil Taxonomy [33]. The authorization number issued by the  
150 Chico Mendes Institute for the Conservation of Biodiversity for the conduct of this  
151 study was: (Authorization SISBEn, 54221-1)

152

153 **RESULTS AND DISCUSSION**

154 The three profiles open along the sampled transect of the Serra da Mocidade  
155 National Park delimited three different types of soils: (i) Entisols Fluvents, (ii) Entisols  
156 Quartzipsamments and (iii) Yellow Ultisols (Figure 2). All of them were characterized  
157 as chemically poor (Table 1) and with high sand contents (Table 2). The results found in  
158 the forest type classified as Treed and Forested shade-loving (La + Ld), 3-4 month  
159 flooded in the year, are associated with the Entisols Fluvents, while Entisols  
160 Quartzipsamments and Yellow Ultisols are associated, respectively, to the Area of  
161 Ecological Tension (LO) and Open Ombrophylous Forest (Ab+As) (Table 3). These  
162 hydro-edaphic characteristics are similar to those reported in the Viruá National Park  
163 [21-22], a region with similar ecological characteristics to the Serra da Mocidade,  
164 strongly indicating that soils with higher levels of sand, low nutrient contents and higher  
165 flooding periodicity can define oligotrophic forest types with lower structural patterns  
166 (vertical and horizontal), in counterpoint to areas free of flooding processes, such as  
167 ombrophilous forests (Figure 3).

168

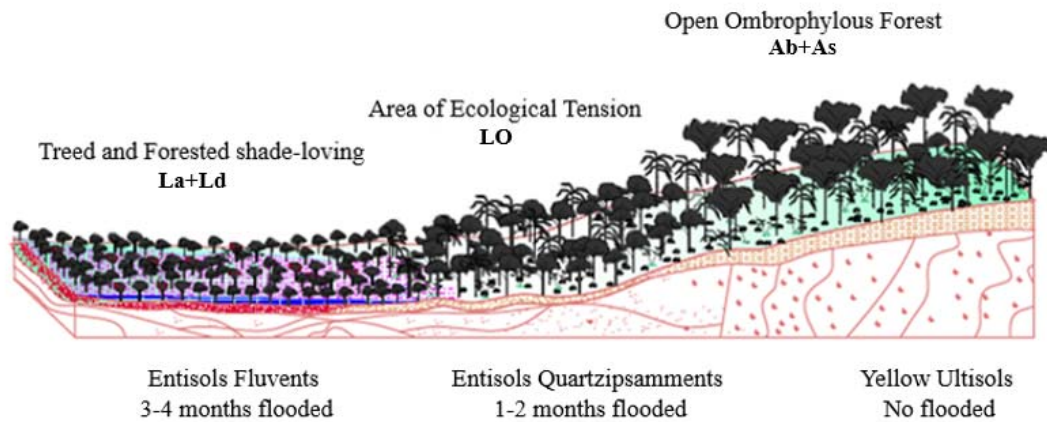


169 **Figure 2- Soil profiles opened in the Serra da Mocidade**  
170 **National Park.**

171 Where the profiles area: **A= Entisols Fluvents (Treed and Forested shade-loving La+Ld)** **B= Entisols**  
172 **Quartzipsamments (Area of Ecological Tension LO)** and **C= Yellow Ultisols (Open Ombrophylous**  
173 **Forest Ab+As).**

174

175 **Figure 3-** Conceptual model of the three forest types characterized by the soil classes  
 176 and flooding periodicity in a transect in the Serra da Mocidade National Park,  
 177 northern Brazilian Amazonia.



178 Entisols Fluvents can be considered as a low developed soil formed by  
 179 quaternary sediment deposits, where drainage varies from moderate to imperfect, and it  
 180 is very influenced by the outflow of the water table [37]. In the study area, this soil class  
 181 was characterized by the predominance of high levels of fine sand followed by the silt  
 182 (Table 2), associated with mosaics of treed and forested shade-loving, which are  
 183 oligotrophic forest environments with low structural expression that naturally dominate  
 184 part of the rio Branc-rio Negro basin [38-40]. The pH in this environment showed a  
 185 tendency to reduce as a function of soil depth, due to the high levels of fine sand, which  
 186 facilitates the processes of water percolation and nutrient leaching [41]. The available  
 187 phosphorus also presented a decrease with depth, being this a process associated to  
 188 alluvial sediment entrainment condition of the high parts of the topographic gradient,  
 189 considering that the parts of lower altitude are characterized by more restrictive soils (3-  
 190 4 months flooded) that may eventually accumulate higher levels of fertility in the early  
 191 layers in contrast with deeper layers [26].

192 Our sampling in the profile of this soil class indicated that the organic matter had  
 193 the highest values in the first sampling layer (0-20 cm). This result is in agreement with  
 194 that presented [25-42], where the authors suggest that soils with higher elevations tend  
 195 to have higher clay contents compared to lowland soils, but the organic matter contents  
 196 are higher in the first layers of lowland soils due to the strong drag provided by the  
 197 topography of terrain. Concerning to the physical properties of this soil class situated in  
 198 the La+Ld forest type, it was verified higher concentrations of silt and fine sand, which  
 199 are textural particles fully compatible with natural lowland environment [43].

200 Entisols Quartzipsamments is characterized as a soil under Area of Ecological  
201 Tension (LO), 1-2 months flooded in the year, and it can be described as a soil class  
202 extremely weathered, much quartzous, where almost all the clay is destroyed by  
203 acidolysis, or sandy deposits formed by wind phenomena, occurring in flat reliefs or  
204 basin reliefs or even in soft undulating reliefs [36-37]. This class of soil presented high  
205 levels of fine and coarse sand (Table 2), where these physical characteristics are  
206 associated to the formation processes of this environment, especially by the presence of  
207 small streams that precede the first undulating steps of the Cumarú Mountain, with  
208 undulations which aid the accumulation of alluvial material derived from the highest  
209 part. Thus, this soil type is related to the hydrological processes of sediment trapping, as  
210 also observed in the region of the National Park of Viruá (Roraima), in similar  
211 environments to those found in Serra da Mocidade [21].

212 The pH values determined for this soil class in the study area are in line with the  
213 standards [35]. An analysis along the soil profile in this forest type allowed to  
214 understand that there is a slight increase in the pH values from the most superficial layer  
215 (0-20cm) to the deepest ones (20-40cm, 40-60cm) and, consequently, a reduction in  
216 exchangeable and potential acidity (Table 1). This is a process fed by the infiltration of  
217 exchangeable bases or increase of organic matter, as previously established [44].  
218 Likewise, the values of available phosphorus presented a decrease between the second  
219 (20-40 cm) and the third layer (40-60 cm), being a strong indicative of the reduction of  
220 this element along the vertical soil profile, as observed [45].and it can act as a limiting  
221 element in the larger / smaller vertical and horizontal structuring of the forest.

222 Organic matter also declines from the superficial to the deeper layers of this soil  
223 class in the study area. This same observation was reported in the Viruá National Park,  
224 with the authors suggesting that the topography of the terrain, especially those with soft  
225 ripples, may retain organic matter in the superficial layers of the soil due to the sediment  
226 trapping or the temporal outcropping of the water table [21] which are the same  
227 environmental characteristics observed in the ecotone (LO) of the Cat's Trail. In the  
228 same sense of the organic matter, the CEC also has a reduction pattern from the most  
229 superficial to the deepest layers, presenting a CEC saturation problem with the  
230 exchangeable Al, being common in this soil type, which can be aggravated by depth due  
231 to the decrease of organic matter in the soil and exchangeable bases such as  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$



232 and  $K^+$ , which would limit the development of the roots of the plants and affect the  
233 structure of the forest [46].

234 The Yellow Ultisols is characterized as a soil type flooding free, with strong  
235 presence of Open Ombrophylous Forest (Ab+As), with high contents of coarse sand and  
236 clay (Table 2) the formation factors of this soil class are similar to that of the Oxisols,  
237 with the same geomorphological characteristics and natural vegetation, but with a  
238 textural gradient [37]. The pH values found in this environment are slightly acidic and  
239 there is not much difference between the layers (Table 1). This process may be  
240 happening due to the absence of both water table outcrops and temporal flooding in this  
241 area [41-47]. The content of organic matter found in this soil type was high in the first  
242 layer, decreasing drastically towards the deeper layers. This result indicates a direct  
243 relationship with the CEC values found in this soil type, within the relational  
244 congruence [48] where organic matter and clays are the edaphic parameters with the  
245 greatest contribution to the formation of CEC values.

246 In this same analytical path, the concentrations of the micronutrients observed in  
247 the profile of this soil highlight the higher concentration of Fe in the first two layers (0-  
248 20 cm and 20-40 cm), being this element the main constituent of the structure of the  
249 clays [49]. This chemical characteristic was also observed in the ombrophilous forests  
250 of the Viruá National Park [23] suggesting that higher Fe contents in the ombrophilous  
251 forests of regions under the influence of treed and forested shade-loving mosaics may  
252 be due to the high presence of mineral particles (oxides of iron) derived from the  
253 organic matter deposited on the soil in litter form. This indicates that both Fe and the  
254 other micronutrients (Zn, Mn, B, Cu) have an important role in the nutrient cycling of  
255 this forest environment, but without a clearly defined role as a characterizer of forest  
256 types. This evidence the large range of uncertainties that still persist in the evaluations  
257 on the relationships between hydro-edaphic conditions and their role in the construction  
258 of Amazonian ecosystems. In this way, it is inferred that a better spatial distribution of  
259 the pedo-phytosociological studies, addressing peripheral regional gaps, can help us to  
260 generate environmental standards (topographic gradients, periodicity of flooding, soil  
261 classes) that more accurately configure the particular structural and floristic  
262 characteristics of different forest types, allowing better accuracy in biomass/carbon  
263 estimates, and giving the real importance of the Amazonia in the context of the global  
264 warming mitigation.

265

266 **Table 1 - Chemical attributes determined in three profiles along a topographic gradient**  
 267 **located in the Serra da Mocidade National Park, in the north of the Brazilian Amazonia**  
 268 **in 2018.**

Depth	pH	OM	P	Cu	Fe	Zn	Mn	B	K	Ca	Mg	H+Al	Al	SB	CEC	Sat.	Sat.
(cm)	H <sub>2</sub> O	g/kg		.....mg/kg.....		.....mg/kg.....						.....cmolc/Kg.....				Bases	Al
																V%	m%
<b>Entisols Fluvents</b> – Treed and Forested shade-loving (La+Ld)																	
0-20	5.1	14	3	6.80	92.00	8.20	3.00	0.43	0.10	0.20	0.10	3.40	0.20	0.40	3.80	11	33
20-40	5.2	7	2	6.70	37.20	8.05	1.40	0.25	0.06	0.10	0.10	2.80	0.20	0.26	3.06	9	43
40-60	4.8	5	2	4.60	14.20	5.80	1.10	0.24	0.06	0.10	0.10	2.50	0.20	0.26	2.76	9	43
<b>Entisols Quartzipsamments</b> – Area of Ecological Tension (LO)																	
0-20	4.6	23	3	1.60	9.80	5.65	15.40	0.26	0.20	0.30	0.10	6.40	0.40	0.60	7.00	9	40
20-40	4.9	9	3	2.10	18.60	3.80	2.40	0.38	0.15	0.30	0.10	4.20	0.30	0.55	4.75	12	35
40-60	4.9	5	2	2.00	19.00	3.60	1.20	0.35	0.13	0.30	0.10	3.80	0.20	0.53	4.33	12	27
<b>Yellow Ultisols</b> – Open Ombrophylous Forest (Ab+As)																	
0-20	4.6	11	3	2.90	106.00	5.95	6.50	0.34	0.15	0.60	0.20	4.70	0.20	0.95	5.65	17	17
20-40	4.7	5	2	2.10	102.00	4.30	1.90	0.32	0.12	0.20	0.10	3.40	0.30	0.42	3.82	11	42
40-60	4.6	5	1	0.70	80.00	3.45	2.00	0.27	0.06	0.10	0.10	3.40	0.20	0.26	3.66	7	43

269 Where: OM = organic matter, P = Phosphorus; Cu = Copper, Fe = Iron, Zn = Zinc, Mn = Manganese, B =  
 270 Boron, K = Potassium, Ca = Calcium, Mg = Magnesium, H + Al = Acidable exchangeable, Al =  
 271 Aluminium exchangeable, SB = Sum of bases, CEC =Cationic Exchange Capacity, V = Saturation by  
 272 Bases, m =Saturation by Aluminium.  
 273

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 280

281 **Table 2 - Physical attributes determined in three profiles along a topographic gradient**  
 282 **located in the Serra da Mocidade National Park, northern Brazilian Amazonia in 2018.**

Depth	Arg	Sil	ArT	ArG	ArF
(cm)		.....%			
<b>Entisols Fluvents</b> – Treed and Forested shade-loving (La+Ld)					
0-20	13.9	19.1	67.0	7.0	60.0
20-40	14.2	16.8	69.0	4.0	65.0

40-60	14.2	16.8	69.0	4.0	65.0
<b>Entisols Quartzipsamments – Area of Ecological Tension (LO)</b>					
0-20	15.7	11.3	73.0	20.0	53.0
20-40	17.4	9.6	73.0	21.0	52.0
40-60	16.9	8.1	75.0	23.0	52.0
<b>Yellow Ultisols – Open Ombrophylous Forest (Ab+As)</b>					
0-20	15.4	3.6	81.0	51.0	30.0
20-40	20.3	6.7	73.0	42.0	31.0
40-60	25.0	6.0	69.0	37.0	32.0

283 **Where:** Arg Clay (<0.002mm), Sil Silt (0.053-0.002mm), Total ArT\_Area, ArG\_ Thick Sand (2.00-  
284 0.210mm), ArF\_ Fine Sand (0.210-0.053mm).  
285

286 **Table 3 -** Soil classes, flood periodicity and structural parameters (DBH and total  
287 height) of the forest types observed in the sampling transect formed by the Cat's Trail,  
288 Serra da Mocidade National Park. Where: La + Ld = Mosaic of treed and forested  
289 shade-loving; LO = Area of ecological tension between forested shade-loving and  
290 ombrophylous forest; Ab + As = open ombrophylous forest associated with the first  
291 steps of the Cumaru Mountain. Different uppercase (Trees, ANOVA followed by Tukey  
292 test) and lowercase (Palms; Test t) letters in the columns indicate discrepancies ( $\alpha =$   
293 0.05) between the values of the taxonomic groups.

Forest Type	Density (ind ha <sup>-1</sup> )		DBH (cm)		Ht (m)	
	Trees	Palms	Trees	Palms	Trees	Palms
La+Ld	940	0	13.7± 3.3 A	-	12.2±2.3 A	-
LO	710	45	17.3± 7.4 B	14.5±3.5 a	17.7±2.7 B	17.5±1.9 a
Ab+As	423	85	20.9±12.9 C	18.5±6.5 b	18.3±4.0 B	16.6±3.2 a

294 (\*) DBH = diameter at breast height (cm) and Ht = total height (m)  
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## 304 CONCLUSION

305 We conclude that each soil class determined in this study has a strong  
306 association with the topographic gradient sampled in the study area situated on Serra da  
307 Mocidade National Park, where lower altitude environments with larger flooding

308 periods are related to forest types of lower structural pattern (e.g. tree and forested  
309 shade-loving) preferentially on oligotrophic soils (poor and sandy). These  
310 characteristics indicate the formation of environments influenced by continuous hydro-  
311 edaphic and geological processes, where seasonal flooding and sediment trawling are  
312 part of the process of formation of the main forest types in the study area. Therefore,  
313 edaphic factors and flooding periodicity are environmental characteristics that act as  
314 environmental filters **wich** are important in the formation of the landscape in this region  
315 of rio Branco-rio Negro basin. These results improve our understanding of the  
316 environmental factors that determine different forest types in this region of the  
317 Amazonia, where environments with higher hydro-edaphic restrictions are a strong  
318 indicator of forest types with lower vertical and horizontal structure.

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333

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