

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**A ESTRUTURA DA FLORESTA DE VÁRZEA DO BAIXO PURUS E SUA
RELAÇÃO COM A DURAÇÃO DA INUNDAÇÃO**

BRUNO GARCIA LUIZE

Manaus, Amazonas
Novembro, 2010

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RELAÇÃO COM A DURAÇÃO DA INUNDAÇÃO**

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Dissertação apresentada ao
Instituto Nacional de Pesquisas da
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para obtenção do título de Mestre
em Biologia (Ecologia).

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Sinopse:

Estudei a diversidade da comunidade de árvores nas florestas inundáveis do baixo Purus, RDS Piagaçu Purus. Avaliei o gradiente de inundação e a distância como fatores influenciando na estruturação da comunidade.

Palavras Chave: Gradiente ambiental complexo; Filtros ambientais; limitação a dispersão; Florestas aluviais; Várzea Amazonica.

Dedicatória

A Mãe, Amar

Dedico à esta forte mulher que hoje é anjo ao meu lado

Tua energia e amor a mim são como Gaia a grande mãe da vida

À toda a família; este trabalho é para vocês: Denyze, Marcilio, Mariana e Ana Paula e

Emanuel

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Resumo

Nas planícies de inundação dos grandes rios da região Amazônica ocorrem florestas aluviais, ricas em espécies de árvores tolerantes a períodos de alagamento de até oito meses a cada ano. Utilizando dados de inventários botânicos com árvores ≥ 10 cm DAP, em 16 parcelas de 0,315 ha, descrevemos o padrão de distribuição da diversidade α de árvores em relação ao gradiente ambiental de profundidade de inundação. Também avaliamos a influência do ambiente e do espaço geográfico na variação da composição de espécies entre locais das florestas aluviais na paisagem de várzea do baixo rio Purus, Amazonas. Amostramos 2 951 árvores de 304 espécies e obtivemos como diversidade α de Fisher um valor de 85.05. A diversidade de árvores é relacionada inversamente com o aumento da profundidade de inundação. A dominância em cada parcela aumenta diretamente com a profundidade de inundação. A dissimilaridade florística é alta e mais da metade da variação na composição florística é explicada pela variação na profundidade de inundação e na distância geográfica entre os pares de parcelas. A maioria das espécies comuns não esteve associada a um habitat específico na várzea. Ao longo do gradiente de profundidade de inundação, além de ocorrer redução no número de espécies também ocorre a substituição das espécies que participam da comunidade. O estudo do padrão de distribuição da diversidade ao longo de gradientes de inundação é necessário para o conhecimento da estruturação e para manutenção das espécies em florestas alagáveis na Amazônia.

Abstract

Forests occurring along the floodplains of the major rivers in the Amazon region harbour a diverse tree community. Tree species in these forests cope with a yearly seasonal flooding which can last up to eight months. It is therefore expected that environmental conditions limit specie occurrences. We describe the distribution pattern of α diversity of trees in relation to the environmental gradient of inundation. We also evaluated the influence of environment and space in the species composition among sites in the forest landscape of alluvial floodplain of the lower Purus river, Amazonas, Brazil. Using data from botanical inventories of trees ≥ 10 cm DBH, 16 plots of 0.315 ha, we sampled 2 951 trees in 304 species and obtained a Fisher diversity (α) of 85.05. The diversity of trees is inversely related to flood depth. The dominance of each plot directly increases with flood depth. The floristic dissimilarity is high and variation in flood depth and geographic distance between pairs of plots explain more than half of the variation in floristic composition. The most common species were not associated with a specific habitat in the floodplain. Along the gradient of inundation the tree community shows a decreasing number of species together with species replacement. The study of the distribution pattern of diversity along gradients of flooding is necessary for understanding the structure and maintenance of flooded forests in Amazonia.

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Introdução Geral

Florestas tropicais abrigam alta diversidade de espécies de árvores por unidade de área. Nestas regiões, a diversidade de espécies varia, parcialmente, em função dos limites de dispersão (Hubbel 2001), filtros ambientais (Ferrier et al. 2007; Tuomisto and Roukolainen 2006) e filtros de interação (e.g., competição, predação, mutualismo) (Wright 2002). De maneira simplificada, pode-se dizer que se as espécies pudessem ocorrer em todos os locais, ou seja, se os limites de dispersão, filtros ambientais e filtro de interação tivessem pouca influência na diversidade, então diferentes locais exibiriam uma mesma composição. Estes locais teriam então o mesmo peso na manutenção da biodiversidade (Legendre et al. 2005).

No entanto, as espécies de árvores das florestas tropicais não se distribuem de maneira homogênea pela paisagem e a composição de espécies de cada comunidade é afetada pela combinação de vários processos ecológicos (Duivenvoorden et al. 2002).

As florestas tropicais da Amazônia podem ser classificadas como florestas não alagáveis (florestas de terra-firme), que ocorrem em terrenos relativamente mais elevados e florestas alagáveis (florestas aluviais) que ocorrem nas planícies de inundação às margens dos grandes rios (Pires and Prance 1985; Terborgh and Andresen 1998). As florestas aluviais estão sujeitas a alagamentos sazonais ocasionados por um pulso de inundação devido ao transbordamento marginal dos grandes rios da Amazônia (Junk 1989). As árvores que ocupam estas florestas têm adaptações fisiológicas, morfológicas e ecológicas para sobreviver às condições ambientais variáveis destes ambientes (Parolin et al. 2004). Algumas espécies de árvores suportam enchentes superiores a 9 m de profundidade e períodos de submersão que chegam a oito meses por ano. Tais condições podem facilmente causar o apodrecimento de raízes e a diminuição do crescimento das espécies lenhosas não adaptadas (Ferreira et al. 2007). Porém, as limitações ambientais ocasionadas pelas enchentes anuais não são as únicas limitações impostas às espécies arbóreas nas planícies aluviais. Nos terrenos sedimentares recém expostos para a colonização pelas plantas, a alta incidência de radiação solar e a competição com gramíneas de rápido crescimento são intensos (Wittmann and Junk 2003). Outra importante limitação ambiental nas florestas aluviais é a ocorrência de períodos de estiagem coincidentes

com a fase que a floresta não está alagada e que pode causar estresse hídrico nas plântulas e juvenis de espécies pouco adaptadas à falta de água (Parolin et al. 2010). Estes fatores são determinantes no processo de regeneração dessas áreas.

As florestas aluviais que ocorrem nas margens dos grandes rios de águas barrentas originados nos Andes são conhecidas como florestas de várzea (Prance 1979). As florestas de várzea estão nos terrenos mais recentes da bacia Amazônica e os rios que passam por estas planícies carregam grande quantidade de sedimentos provenientes do processo de erosão de seus leitos. O pulso de inundação anual, ao qual as florestas de várzea estão sujeitas, confere a estas áreas uma alta fertilidade do solo através da deposição dos sedimentos da erosão dos Andes que são carreados pelos rios até as planícies aluviais.

As enchentes anuais e as mudanças do leito do rio ocasionam erosões nas planícies de inundação e conferem caráter dinâmico às formações vegetais nas várzeas (Salo et al. 1986; Kalliola et al. 1991). Assim, é possível encontrar manchas de floresta de várzea em diferentes estádios sucessionais (Foster 1990; Worbes et al. 1992; Wittmann et al. 2004). Diferenças de sedimentação na planície de inundação propiciam a formação de pequenas variações topográficas que, associadas à amplitude do pulso de inundação, causam heterogeneidade ambiental (Albernaz et al. 2007).

A diversidade e a composição de espécies de árvores em um determinado local da floresta aluvial é influenciada pelo pulso de inundação. Em geral, locais que permanecem inundados por mais tempo e aqueles com maior profundidade de inundação são os locais que uma menor quantidade de espécies consegue ocupar (Ferreira 1997; Wittmann et al. 2002). A ocorrência de gradientes ambientais e sua influência na diversidade de espécies é bastante estudada seja em escala local e de paisagem (e.g. gradiente altitudinal), como em escala continental e global (e.g. gradiente latitudinal) (ver Lomolino et al. 2006).

A descrição do padrão de variação da diversidade em comunidades ao longo de gradientes levou a formulação de diferentes hipóteses a respeito dos processos que explicam a variação na diversidade das espécies entre locais (eg. produtividade, limitações ambientais, diferenciação de nicho) (ver Lomolino et al. 2004). O padrão de distribuição da diversidade de árvores ao longo de gradientes ambientais, ocasionado por variações na duração do período e na profundidade de inundação já foi explorado nas florestas aluviais da Amazônia, tanto para as florestas de várzeas

(Ayres 1993; Wittmann et al. 2002) quanto para as florestas de igapó (Ferreira and Strohlgren 1999; Ferreira 2000). No entanto, apenas o estudo de Wittmann e colaboradores (2006) avaliou a influência dos limites de dispersão na estrutura das comunidades de árvores nas florestas de várzea da Amazônia, indicando um efeito espacial na escala da bacia amazônica.

Objetivo

Neste estudo analisamos o padrão de variação na diversidade local de árvores ao longo do gradiente de inundação na paisagem de floresta de várzea do baixo rio Purus. A similaridade florística foi relacionada com a diferença de profundidade de inundação e com a distância geográfica entre localidades determinando a contribuição relativa do gradiente ambiental (i.e., profundidade de inundação; duração do período de inundação) e dos limites de dispersão (i.e., distância geográfica) na variação da diversidade e da composição de espécies arbóreas. Descrevemos o padrão de distribuição das espécies ao longo do gradiente de inundação e avaliamos a possibilidade de espécies dominantes distribuindo-se por toda a paisagem independentemente da condição ambiental. As seguintes questões foram abordadas: 1) Qual a relação entre o gradiente ambiental de profundidade da inundação e a diversidade alfa de árvores?; 2) Qual o papel do espaço ambiental e do espaço geográfico na estruturação da variação da diversidade alfa e da dissimilaridade florística?; 3) Existe preferência das espécies comuns a determinadas posições ao longo do gradiente ambiental de inundação?

1 **Manuscrito redigido segundo as normas da revista Ecography**

2

3 **ENVIRONMENTAL AND SPATIAL FACTORS ON TREE SPECIES RICHNESS**
4 **AND COMMUNITY STRUCTURE OF FLOODED FORESTS IN PURUS RIVER,**
5 **CENTRAL AMAZON**

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15 **Abstract**

16 In the floodplains of major rivers in the Amazon region occur alluvial forests rich in tree
17 species tolerant to flooding periods of up to eight months each year. Using data from
18 botanical inventories of trees ≥ 10 cm DBH, 16 plots of 0.315 ha, we describe the
19 distribution pattern of α diversity in relation to the environmental gradient of inundation.
20 We also evaluated the influence of environment and space in the species dissimilarity
21 composition among sites in the forest landscape of the alluvial floodplain of the lower
22 Purus river, Amazonas, Brazil. We sampled 2 951 trees in 304 species and obtained a
23 Fisher diversity (α) of 85.05. The diversity of trees is inversely related to increase in
24 flood depth. The dominance of each plot directly increases with flood depth. The
25 floristic dissimilarity is high and variation in flood depth and geographic distance
26 between pairs of plots explains more than half of the variation in composition
27 dissimilarity. 87% of the most common species was not associated with a specific
28 habitat in the floodplain. Along the gradient of inundation the tree community shows a
29 decreasing number of species together with species replacement. The study of the
30 distribution pattern of diversity along gradients of flooding and distance of localities is
31 necessary for understanding the structure and maintenance of the flooded forests in
32 Amazonia.

33 The Amazon river basin occupies more than 6.8 million km², draining the equivalent of 25% of
34 the surface area of South America (Goulding et al. 2003). The seasonality of the rain regimens
35 associated with the low declivities causes annually inundations that transform the land
36 environments on the edges of the larger Amazonian rivers into aquatic environments (Junk et al.
37 1989). Within these floodplains and terraces there occur alluvial tropical forests (known as
38 *várzea* and *igapó*, *sensu* Prance 1979). The plants that establish themselves in these
39 environments possess adaptations for aquatic-terrestrial life, in function of the regular and
40 predictable occurrence of the flood pulse (Junk 1989; Junk 1997; Parolin et al. 2004). The flood
41 pulse justifies the establishment of a complex environmental gradient (*sensu* Whittaker 1967)
42 represented by the duration and depth of the flooded area. This environmental gradient has
43 consequences in the structure of biological communities and is a determining factor in local
44 (Ayres 1993; Ferreira and Strohlgren 1999; Wittmann et al. 2002) or regional (Wittmann et al.
45 2006) diversity of trees.

46 Seasonal flooded forests cover approximately 144 000 km² of the Central Amazon Region
47 (Hess et al. 2003). The geomorphological processes of erosion, sedimentation, and annual flood
48 pulse confer a dynamic character on the floodplains of the white-water rivers (*várzea*)
49 influencing the existence of plants communities in different successional states (Salo et al.
50 1986; Foster 1990; Worbes et al. 1992; Wittmann et al. 2004). The *várzea* landscapes are
51 formed by sediments rich in nutrients, eroded of the Andes and carried by the white-water rivers
52 to lowlands (Irion et al. 1997). The *várzea* forests of the Amazon contain the largest collection
53 of trees species that are flood-tolerant in the world floodplain forests (Wittmann et al. 2006),
54 hosting a great diversity of adaptations and arboreal species with the capacity to withstand
55 extreme flooding with more than eight meters of depth and until six months of permanence
56 (Junk 1997).

57 The process through which the community structure is created and maintained and the manner
58 in which the species composition varies among the habitats is fundamental for understanding
59 the functioning of the ecosystems for the conservation of the biodiversity and for the efficient

60 allocation of economic resources in territorial management (Ferrier 2002; Legendre et al. 2005).

61 The environmental factors that influence the structure of the tree communities in the tropical
62 forests have been amply discussed in the literature and bear evidence to the complexities of
63 these communities. Many times not even the different combination of variables is capable of
64 explaining much with regards to the structure of the diversity in these communities (eg.
65 Duivenvoorden et al. 2002; Chave 2008). The difficulty in understanding the factors that
66 determine the structure of the arboreal community in the tropical forests is, in part, related to the
67 fact that the majority of tree species occur in low densities in an ecosystem with elevated
68 environmental heterogeneity (Pitman et al. 2001).

69 According to Tuomisto and Ruokolainen (2006), three ecological hypotheses with regards to
70 the structure of the communities have special relevance for forest communities. The first
71 implies that the species composition among localities float in a random fashion and is not
72 related to environmental factors, or rather, the same species present similar relative abundances
73 in geographically closer locations due to the limitation of species dispersal (Hubbell 2001). The
74 second, called the oligarchy hypothesis (Pitman et al. 2001), implies uniformity of forest
75 composition among localities and the dominance of oligarchic groups of species distributed
76 regardless of environmental conditions and habitats patches along the landscape (Pitman et al.
77 2001; tuomisto and Ruokolainen 2006). The third hypothesis considers that the distribution of
78 species is related to the environmental conditions, assuming that locations with similar
79 environmental conditions present greater floristic similarity than locations that differ in their
80 environmental conditions (Gentry 1988, Tuomisto et al. 1995).

81 These hypotheses, considered separately, seem to not explain the variation of the structure of
82 arboreal communities of *várzea* forests along the environmental and geographical gradients. For
83 these forests a high dominance of species is expected in comparison to the upland forests, given
84 that a lower number of species is adapted to the conditions of these environments (Pires and
85 Prance 1985). It is still expected that the variation of the diversity and the floristic composition
86 along the landscape be strongly related to the duration gradient and flooding depth throughout

87 the year (Ayres 1993; Ferreira and Stohlgren 1999; Wittmann et al. 2002), selecting species
88 tolerant to consecutive flooding. On the other hand, comparisons indicate high local floristic
89 heterogeneity among patches of forest in the *várzea* (Terborgh and Andresen 1998), which
90 could mischaracterize the hypothesis of oligarchic species dominating extensive areas of forest.
91 The great majority of studies formalize predictions with respect to the diversity in relation to
92 environmental determinism (Ferreira and Stohlgren 1999; Wittmann et al. 2002), with only the
93 study by Wittmann and collaborators (2006) evaluating the effect of geographical distance in
94 the floristic composition of the *várzea* forest on a continental scale for the white-water rivers of
95 the Amazon Basin.

96 In this study, we analyzed on a local scale and on a landscape scale the structure of arboreal
97 communities of *várzea* forests in the region of the lower Purus River. We considered to this end
98 the three ecological hypotheses previously presented. Thus, we explored the following
99 questions: 1) What is the relationship between the environmental gradient of flooding depth and
100 the alpha diversity of trees; 2) What is the role of environmental distance and geographical
101 distance in the structure and in the variation of the alpha diversity and of the floristic
102 dissimilarity; 3) Does there exist preference for common species to determined positions along
103 the environmental gradient of flooding?

104 **Methodology**

105 *Area of Study*

106 The landscape we studied is located in the region of the lower Purus River, in the Central
107 Brazilian Amazon (Figure 1). The study was conducted in alluvial forests within the limits of the
108 Piagaçu-Purus Sustainable Development Reserve RDS-PP, a state conservation unit of the
109 sustainable use group (de Deus et al. 2003). The Purus River is a white-water river representing
110 5% (375 000km²) of the area of the Amazon Basin and possessing approximately 21 000km² of
111 floodplains along its edges, constituting the largest area of floodplains among the tributaries of
112 the Amazon River (Goulding et al. 2003). The amplitude of the rainy period of the Purus River

113 varies annually at around 10 m in the city of Beruri, Amazonas, Brazil (HidroWeb 2010). The
114 rainy period occurs between December and February, with the peak of flooding from the
115 months of May to July. Once past the peak of the rainy season and flooding the water-levels of
116 the river begin receding, reaching their lowest levels in the months of October and November
117 (Haugaasen and Peres 2006). The total annual precipitation in the region of the lower Purus
118 River is around 2 000 mm and the average temperature is around 24 °C . Recent studies suggest
119 that the region of the lower Purus River (at approximately 62°, 63° long.) present a high
120 arboreal species richness, both for flooded forests and for upland forests (Albernaz et al. 2007;
121 Hopkins 2007). However, few projects have sampled the forests of this region (Haugassen and
122 Peres 2006; Albernaz et al. 2007).

123 *Sampling of the vegetation*

124 Between August and December of 2009 we inventoried the arboreal vegetation in 16 plots of 3
125 125 m² (0.3125 ha), totaling an area of 5 ha. The plots had a rectangular format with dimensions
126 of 125x25m and were oriented in such a way that their main axis was contained in the lowest
127 variation of relief and guaranteed homogeneity of sample units. The location of the plots
128 followed two criteria: 1) spatial dispersion of the plots; 2) environmental gradient range. In
129 order to guarantee spatial dispersion we adopted a minimum distance of 1 km between plots. In
130 order to guarantee the range of the environmental gradient each plot was to present different
131 depths of flooding (1.6 to 9.1 m in 2009 flood season) until the entire environmental gradient
132 was contemplated.

133 All of the individual trees with DBH \geq 10 cm (diameter at breast height at 1.30 m) were marked
134 and numbered with aluminum plates. Botanical samples from the trees in the plots were
135 collected and botanical determinations were done by comparison with the material from the
136 INPA (National Institute for Amazonian Research in Manaus, Brazil) herbarium and, when
137 determination was not possible, morphotyping of the materials was performed. For the
138 individuals that presented fertile structures, samples were collected with duplicates which were
139 later deposited in the INPA herbarium. Of the total of sampled individuals, 73% were identified

140 at the species level, 25% were morphotyped at the genus level, and just one percent was
141 morphotyped at the family level.

142 ***Environmental Data***

143 Each vertex of the sub-plots was geo-referenced with the aid of the GPS Garmin® 60CSx
144 (Datum WGS 84; decimal degrees) instrument, forming a Geographical Information System
145 (GIS). The central point of each plot was utilized to calculate the linear geographical distance
146 between the plot pairings (Geographical Distance Matrix, GDM). In each sub-plot three
147 individuals were selected, whereby the height of the water mark left on the trunk during the
148 most recent flooding was measured (July-August 2009). The measurements of the water marks
149 were taken with the aid of a graduated tape measure with a minimum scale of 5 centimeters.
150 The flooding of 2009 was about 1.87 ± 0.92 m above the average historical maximum level in
151 Beruri, Amazonas (HidroWeb 2010). We considered that the measurement of the water mark on
152 the tree trunk represents the maximum depth of the most recent flood season and assumed that
153 the greater the flooding depth, greater the period in which the *várzea* forest remains flooded.
154 We calculated the Euclidean distance in meters of depth among the inventoried plots
155 (Environmental Distance Matrix, EDM). We calculate all distance matrixes in R software (R -
156 Development Core Team 2008).

157 ***Data analysis***

158 The total number of species listed in each plot was used as the value of species richness
159 observed (S_{obs}). Possible differences in the values of species richness observed could be related
160 to the variation of the number of individuals sampled (Gotelli and Colwell 2001). Thus, we
161 calculated the numerical species richness (S_{rar}) per individual added to the sample with the use
162 of rarefaction curves computed with the computer program EstimateS (Colwell 2006). We
163 utilized as a base of comparison S_{rar} when the number of individuals reached 100 trees per plot.
164 The data from S_{rar} are more appropriate for testing the ecological hypothesis relative to the
165 restriction of the number of species that occur in the most flooded parts of the *várzea* forest due
166 to the allusion made to the species abundance (Gotelli and Colwell 2001). We evaluated the

167 alpha diversity with the Fisher alpha coefficient (α Fisher) of each plot and of all the plots
168 together as a whole. The α Fisher is a parametric index of diversity that adjusts the distribution
169 of a logarithmic series, which relates the number of species found with a determined abundance
170 in the sample (Magurran 2004). Their values are relatively little impacted by the variation of the
171 sample size and are even robust when the empirical data do not conform to a logarithmic series
172 distribution (Magurran 2004). We calculated the number of unique species (*singletons*) for each
173 plot utilizing information from the species that occurred with just one individual in all the 16
174 plots sampled. We considered *singletons* as being species with low density of individuals per
175 hectare ($< 0.2 \text{ ind} \cdot \text{ha}^{-1}$ in the landscape). We estimated the equitability in the sample through
176 the Berger-Parker Index (Dd), as it is a dominance index that is rather simple and intuitive. Its
177 value represents the most abundant species in each sample and is obtained through the
178 proportion in relation to the total abundance of that particular sample (Berger and Parker 1970;
179 Magurran 2004). We used models of simple linear regression with adjustment of minimum
180 squares to estimate the relation between the environmental gradient and the structural attributes
181 of the *várzea* forest (R Development Core Team 2008).

182 As a measure of variation in the composition of species between the plots we used the Bray-
183 Curtis floristic similarity coefficient (C_{BC}). The resulting dissimilarity matrix is quantitative and
184 considers the values of abundance of the species in the plot. The Bray-Curtis dissimilarity index
185 is the complement of C_{BC} ($1 - C_{BC}$) and varies between zero and one, with zero indicating that all
186 the species are shared with similar relative abundances and one indicating that none of the
187 species are shared between location pairing. The Bray-Curtis similarity index is a quantitative
188 variation of the Sørensen similarity index (Magurran 2004). According to Tuomisto (2010), the
189 complement of the Sørensen index represents an exchange of species between locations
190 (*Whittaker species turnover*). Thus, we considered $1 - C_{BC}$ as being a measure of the magnitude
191 of exchange in the composition of species between locations.

192 In order to verify the relationship between the exchange of species ($1 - C_{BC}$) and the distance of
193 depth (EDM) or the geographical distance (GDM) between the plots, we calculated coefficients

194 of Pearson correlations using the Mantel procedure with 10 000 permutations (R Development
195 Core Team 2008).

196 We reduced to one the dimensions of the floristic dissimilarity matrix with the non-metric
197 multidimensional scaling technique (NMDS). We calculated the Euclidean distances between
198 the plots using the resulting axis values from the NMDS solution. Later, we correlated these
199 Euclidean distances with the original floristic dissimilarity matrix (1- C_{BC}) in order to evaluate
200 the quantity of information from the exchange of species that is retained in the unidimensional
201 NMDS axis. High values of correlations indicate that the values summarized in the axis one
202 scores of the NMDS were maintained as faithfully as possible from the initial 1- C_{BC} matrix.

203 We used multiple linear regressions to relate the values of the NMDS axis with the flooding
204 depth, latitude, and longitude. We partitioned the variation of the resulting model among the
205 explanatory variables and calculated the proportion of the explained variation: 1 – by the
206 environmental variation (flooding depth); 2 – by the variation in geographical space; 3 – by the
207 combination of environmental and spatial variation; and 4 –unexplained by the model. The
208 same procedure of partition of the variation was undertaken for a multiple linear model relating
209 the Fisher alpha diversity index of each location with the flooding depth, latitude, and
210 longitude. For these procedures we used the SAM software (Rangel-Filho et al. 2010).

211 We considered all of the species with a density of $\geq 1 \text{ ind} * \text{ha}^{-1}$ in the sum of the plots as
212 common species in landscape scale ($\sim 900 \text{ Km}^2$) (Pitmann et al. 2001). In order to test whether
213 the oligarchic species (Pitmann et al. 2001) are distributed along the entire landscape without
214 suffering effects of the environmental gradient of flooding, an analysis of indicator species was
215 applied (*indicator value* - IV) (Dufrene and Legendre 1997). We calculated the IV value for the
216 common species in the landscape with the use of the Pc-Ord program (Dufrene and Legendre
217 1997; McCune and Mefford 1999). We classified the sampled plots in two groups of habitats:
218 VA – high *várzea* (*várzea alta*), those plots with an maximum average historical flooding depth
219 of $< 3.0 \text{ m}$ ($n = 7$ locations) and VB – low *várzea* (*várzea baixa*), all the plots with an maximum
220 average historical level of flooding depth of $\geq 3.0 \text{ m}$ ($n = 9$ locations) (Ayres 1993; Wittman et

221 al. 2002); in order to classify the plots we corrected the values of flooding depth measure in the
222 plots due to the flooding of 2009 having presented greater registered levels of flooding for the
223 Amazon Basin (HidroWeb 2010; 187 ± 092 cm above the maximum average historical level in
224 Beruri).

225 Indicator species are defined as the most characteristic species of the given group (Dufrene and
226 Legendre 1997). Thus, the IV value combines the relative abundance with the relative
227 frequency of occurrence of the species in the samples of one of the two groups of locations
228 (Dufrene and Legendre 1997). The IV value was used to indicate whether there is preference
229 between the VA or VB habitats by the species, given a greater association with a determined
230 habitat with a greater IV value. On the other hand, low IV values indicate that the dominant
231 species in the landscape are distributed indifferently among the two habitats. The statistical
232 significance was evaluated by random procedure, where the 16 plots were permuted 10 000
233 times. The common species were directly ordered using the relative abundance value of the
234 species in the plot for the total of common species ($\geq 1 \text{ ind} \cdot \text{ha}^{-1}$) and for the reduced total of
235 common species with a density of $\geq 5 \text{ ind} \cdot \text{ha}^{-1}$. We verified that the group of common species
236 with a $\geq 5 \text{ ind} \cdot \text{ha}^{-1}$ presents a proportion of indicated species similar to the proportion
237 presented by the group to the group of common species with a density of $\geq 1 \text{ ind} \cdot \text{ha}^{-1}$ ($G=2.16$;
238 $p=0.14$). We then presented the direct order only for the common species with a density of ≥ 5
239 $\text{ind} \cdot \text{ha}^{-1}$.

240 **Results**

241 *General Pattern*

242 2 951 individuals with DBH ≥ 10 cm were inventoried, in the five hectares of *várzea* forest in
243 the lower Purus River (Table 1). The sampled individuals belong to 304 species of trees. Our
244 data show two distinct groups of curves of accumulation for the *várzea* forests (Figure 2). The
245 first group, in general, represents the communities sampled in the locations with lesser flooding
246 depth, whereas the second group represents the communities in locations with greater flooding

247 depth (Figure 2; Table 1). The density of trees varied between 406 and 1 171 individuals per
248 hectare and the total basal area varied between 26 and 48 m² *ha⁻¹. These two structural
249 attributes presented a light increase along the gradient of flooding depth (Table 1). However,
250 the adjustment of the linear models shows that the flooding depth was not related to the number
251 of individuals or with the basal area between each location ($r^2 = 0.17$ e $r^2 = 0.03$; $p > 0.05$,
252 respectively).

253 Considering the total number of species registered per plot, the percentage of species
254 represented by one individual varied between 30% and 50% of the species, with the greater
255 percentages being found in the plots that presented the greatest number of species. The species
256 richness in the *várzea* communities varied up to three times from one location to the another
257 (Table 1). The exchange of species was high and only on pair of locations had a value of $1-C_{BC}$
258 < 0.5 (Figure 3). The two plots with the greatest value of similarity among them were in
259 locations with greater flooding depth and lower species richness. Two pairs of locations shared
260 no species and presented $1-C_{BC}$ equal to one. The exchange of species ($1-C_{BC}$) for the total of
261 VB plots varied between 0.45 and 0.98, while for the total of VA plots varied between 0.58 and
262 0.82 (Figure 3).

263 ***Alpha diversity and Environmental gradient***

264 We found an inverse relationship between the flooding depth and the quantity of species present
265 in the community (Figure 4). This relation is maintained as much in the observed values of the
266 species richness (S_{obs}) in each location as well as in the standardized richness values (S_{rar})
267 between the locations. The Fisher α diversity of trees in the *várzea* forest also decreased in
268 function of the increase in the flooding depth (Figure 4). Both the models of species richness
269 and the Fisher α diversity were inversely related to the flooding depth gradient and their
270 coefficients of determination were similar ($B_{std} \sim - 0.80$; see Table 2). For the Fisher α diversity
271 the locations with greater flooding depth presented values between 6 and 26. In locations with
272 lower flooding depth, the Fisher α variation stood between 29 and 43.

273 We found 104 *singletons* (34 % of the species) in the 16 locations sampled. The quantity of

274 species represented by only one individual in the landscape was greater in the locations with
275 lower flooding depth (Figure 4 and Table 2). The Dd index of dominance varied up to four
276 times (Table 1), with the locations with greater flooding depth presenting species with greater
277 values of dominance. *Luehea cymulosa* was the species with the greatest value of dominance,
278 representing 47% of the trees in a location and was found in 40% of the sampled locations.
279 However, 71% of the individuals of *L. cymulosa* were in one single location. The Dd value
280 relative to *L. cymulosa* was removed from the model estimate for characterizing a overlay. The
281 model excluding the Dd value of *L. cymulosa* presented less error in relation to the estimate of
282 the coefficient *b* and a better adjustment of the locations to the line estimate (Figure 4; Table 2).
283 The 14 dominant species in each of the 16 location are among the 31 most common species
284 with a density of $\geq 5 \text{ ind*ha}^{-1}$. The first 31 species of greatest density possess estimates between
285 5 and 41 ind*ha^{-1} for the studied landscape. The species with densities of $\geq 5 \text{ ind*ha}^{-1}$ represent
286 approximately 70% of the sampled individuals, nine of these species occurred in 50% or more
287 of the plots, and six occurred in fewer than 25% of the plots. The common species (density ≥ 1
288 ind*ha^{-1}) represent approximately 90% of the sampled individuals.

289 *Influence of the environment and of the geographical space in the diversity of trees*

290 **Alpha Diversity**

291 Among the three multiple linear models for the prediction of Fisher α diversity, only on the
292 model of the total of the plots was significant (Table 4). The environmental variation and the
293 environmental variation shared with the spatial variation contributed to 65% of the explanation
294 of the variation of the Fisher α model (Figure 5). The quantity of unexplained variation of the α
295 Fisher model is 33% (Figure 5). The values of the Fisher α were inversely related to the
296 flooding depth and to the latitude (Table 4). The longitude of the plot was inversely related to
297 the Fisher α only for the general model and for the VB. The Fisher α models for the group of
298 VB and VA plots were not significant (Table 4).

299 **Beta Diversity**

300 **Mantel Correlation Approach**

301 The floristic dissimilarity ($1 - C_{BC}$) was related to the EDM and was not related to the GDM
302 between the plots (Table 3, Figure 3). For the VA plots there was not any correlation of the
303 values of $1 - C_{BC}$ and the distance of flooding depth, and not at all with the geographical
304 distance. As for the group of VB plots, they presented a correlation between $1 - C_{BC}$ and the
305 distance of flooding depth (Table 3). However, the adjustment of the correlation diminishes in
306 relation to the correlation performed with the information from all the plots (Table 3, Figure 3).
307 The variation of floristic dissimilarity between the VB plots was not correlated to geographical
308 distance (Table 3).

309 **NMDS Approach**

310 The euclidian distance of the NMDS axis correlate 0.82 of the information from the original $1 -$
311 C_{BC} matrix that measures the exchange of species. Proximate values occurred between the
312 solutions of the NMDS axis for the VB ($r = 0.72$) and VA ($r = 0.80$). The partition of the
313 explanation of the multiple linear model, which estimates the values of the NMDS axis, shows
314 that 86% of the variation of the model is explained by environmental variation and by the
315 environmental variation shared with the variation in geographical space (Table 4, Figure 5). For
316 the group of VB plots, 68% of its variation is explained by the variation in the total of the
317 environmental and geographical space summed with the variation explained by the environment
318 only (Table 4, Figure 5). The group of VA plots did not have a significant multiple models as a
319 whole (Table 4). However, the b coefficient estimated for the predictive environmental variable
320 contributed to 12% of the explanation of the multiple models that estimates the exchange of
321 species for the VA plots (Table 4, Figure 5).

322 ***Indicator species***

323 The 16 sampled locations on the lower Purus River included 124 common species with a
324 density of $\geq 1 \text{ ind} * \text{ ha}^{-1}$. These species represent approximately 90% of the individuals and 40%
325 of the samples species. The analysis of indicator species showed 29% of the common species in
326 the landscape having an IV value of ≥ 50 . However, only 29 species had IV values that can be
327 differentiated from the expected chance value ($IV \text{ p} < 0.05$). All of the 29 species considered

328 habitat indicators had an IV value of ≥ 55 . More indicator species were found in the VA forests
329 than in the VB forests (VA: 24 species; VB: 5 species). The same proportion of indicator
330 species of VA and VB is maintained when we evaluate only the species with a density of ≥ 5
331 ind * ha⁻¹ (G=0.193; P=0.686) (Figure 6).

332 The IV values, in general, were greater for the VA indicator species ($57.1 \geq IV \leq 100$), than
333 those found for the VB indicator species ($55.6 \geq IV \leq 76.5$) (Figure 6). *Brosmium lactescens*
334 and *Tabernaemontana cymosa* were the only species to reach the maximum IV value (Figure
335 6). These two species were frequent and abundant in the understore of *várzeas* forests of low-
336 flooding depth (VA). *Pseudobombax munguba* and *Hevea spruceana* had the greatest IV values
337 in the group of plots that represent the forests that remained flooded for the longest periods of
338 time (VB) (Figure 6). These two species are components of the dossel and occur with frequency
339 in the VB forest and, in some cases, in the VA forests.

340 The low frequency of occurrence of the species with greater density helps to explain the local
341 pattern of high heterogeneity in the floristic composition. We observed that even the
342 communities with few rare species presented high floristic dissimilarity, as the dominant
343 species alternate locally. Of the 14 species with greater indexes of Dd dominance (4% of the
344 sampled species), two species were characteristic of VB (*Hevea spruceana* and *Pseudobombax*
345 *munguba*) and four species were characteristic of VA (*Maquira coriacea*; *Hura crepitans*;
346 *Garcinia madruno* and *Virola surinamensis*, see Figure 6). The other eight locally dominant
347 species did not present a distribution conditioned to a habitat and virtually could occur in all
348 *várzea* forest habitats.

349 **Discussion**

350 The diversity of trees in the landscape of the lower Purus River is shown to be relatively high in
351 relation to other inventories taken in *várzea* forests of the Amazon Region. Wittmann and
352 collaborators (2006) compiled 44 floristic inventories of arboreal species for the *várzea* forest
353 of the Amazon Region and listed the occurrence of 918 species. In this study we sampled an

354 area of five hectares and registered the occurrence of 304 species of trees, which could
355 represent up to 1/3 of the regional pool of species richness reported for the forest of the Amazon
356 *várzea*. The Fisher α diversity index for each of the sampling locations in this study varied
357 between 6 and 43. These values are comparable to the Fisher α diversity found by Wittman and
358 collaborators (2006) for the Amazon *várzeas* in general (α Fisher between 10 and 50). These
359 comparisons that consider the plots individually suggest that the diversity of trees of the lower
360 Purus River is relatively high on the local scale. Considering the diversity sampled by the total
361 of the plots presented by Wittman and collaborators (2006), our data show that the diversity of
362 the lower Purus River is high as well on the regional scale. The region of the lower Purus River
363 was recently evaluated as being a void of botanical collection in the Amazon (Hopkins 2007),
364 reiterating the need for botanical collections in this region with the aim of improving the
365 biogeographical characterizations of the Amazonian flora.

366 The structural attributes, tree density, and the total basal area of each sampling location did not
367 vary along the flooding gradient (see Table 1). This result is contrary to the one found in the
368 *várzea* forests of the lower Japurá River (Ayres 1993) and in the *igapó* forests of the Jaú River
369 (Ferreira and Stohlgren 1999), where an inverse relation between the structural attributes and
370 flooding depth was observed. The species richness observed in each sampling location varied
371 strongly along this gradient. The exchange of species was high, indicating heterogeneity in the
372 floristic composition between locations of *várzea* forests, as was also shown in Terborgh and
373 Andersen (1998).

374 The linear models we computed allow for the realization of robust estimates of the values of the
375 diversity attributes for the studied landscape. The richness of tree species, the Fisher α diversity,
376 the number of rare species and the relative abundance of the dominant species in the *várzea*
377 forest in the landscape of the lower Purus River can be predicted with reliability. With these
378 diversity attributes we can infer how many species will be in a given location and how these
379 species share their abundances in the community. The study of the pattern of variation of the

380 abundance curves of the species along the gradient makes possible the formulation of
381 hypotheses for the local structuration of the diversity in these communities (McGill et al. 2007).
382 As a pattern, we observed that the local diversity of arboreal species in the *várzea* is inversely
383 related to the flooding depth in the forest, results similar to those found in *várzea* forests (Ayres
384 1993; Wittmann et al. 2002) and *igapó* forests (Ferreira and Stohlgren 1999; Ferreira 1997) in
385 the Amazon. The number of unique species (*singletons*) in each location also decreases with the
386 increase in flooding. The community of trees sampled in the landscape of the lower Purus River
387 possesses close to 1/3 of the species with densities of $\leq 0.2 \text{ ind*ha}^{-1}$. The dominant species had
388 higher relative abundances in the locations that remained flooded for longer periods of time.
389 Thus, we observed that the communities in the locations with greater flooding possess
390 distributions of abundance of species that resembles the geometric series model. As the flooding
391 depth decreases, the distribution of abundance of species resembles a logarithmic series. In the
392 communities of greater flooding the process of species filling (*pre-emption model*) during the
393 initial stages of succession is possibly the ecological process of greater influence in the local
394 richness of species (McGill et al. 2007; Wittmann et al. 2004). The number of species that will
395 occupy and participate in the community is somewhat reduced due to the limitations brought
396 about by environmental severity (eg. flooding, droughts, and extreme incidence of solar
397 radiation) and the greater competitive capacity of species tolerant to flooding and that are
398 capable of primarily colonizing the environment in early stages of succession.
399 We observed that few species (10%) represent the majority of the individuals (70%) sampled in
400 the landscape of the lower Purus River. The frequency of occurrence of the common species in
401 the locations was low (see Figure 5). Still, the inverse relation between the dominance and the
402 frequency of occurrence may be bringing about an increase in the exchange of species between
403 locations. In the Amazon scale, the floristic dissimilarity between regions of *várzea* forests may
404 be less due to the occurrence of some dominant species found habitually in the inventories
405 (Worbes et al. 1992; Ayres 1993; Nebel et al. 2001; Urrego et al. 1997; Santos and Jardim
406 2006).

407 The flooding depth was the factor most strongly related to the variation in the floristic
408 composition in the *várzea* forests. The neutral theory prediction (Hubbell 2001), which assumes
409 that there is no environmental effect in the variation of the species composition between
410 locations, is not supported by our data. The data also do not support the hypothesis of oligarchic
411 species (Pitman et al. 2001) due to the floristic heterogeneity and a relation between the commun
412 species and the environmental variation. However, the prediction of oligarchic species
413 dominating extended areas of landscape must be evaluated with greater care because a great
414 number of species communs do not show an environmental preference. Our data do not reject
415 the hypothesis of species composition related to environmental conditions. We observed that
416 the two compartments of *várzea* forest that we evaluated (VB and VA) have influences both
417 from the environment and from the geographical space of their communities. However, the
418 roles of each of these variables have different weights along the environmental gradient. In
419 general, the environment had a preponderant role in the variation in species composition
420 between locations. In all our models the unexplained floristic composition variation was the
421 lesser in proportion. These results are different from those found in tropical upland forests (eg.
422 Duivenvoorden et al. 2002, Chave 2008).

423 In the *várzea* forests, the limitation to dispersion seems not to be a limiting ecological factor.
424 The reproductive behavior of many of the arboreal species that fruit during the high-water
425 season (Parolin et al. 2004; Haugaasen and Peres 2005), summed to the morphological
426 characteristics of the seeds are dispersed by fish or by fluctuation (Gottsberger 1978), can
427 guarantee the species greater capacity of dispersion throughout the *várzea* environment. On the
428 other hand, for the high *várzea* forests, the limitation of the species to environmental conditions
429 seems not to be as determinant in the distribution of the species throughout the landscape as for
430 the low *várzea* forests. We must remember that the two compartments of the community of
431 trees in the *várzea* forests we used here are somewhat arbitrary. The species with preferential
432 occurrence in one compartment can, occasionally, occur in the other, conferring a continuous
433 character on the community of trees in the *várzea* forests, in accordance with the Gleason

434 concept of open communities.

435 In the *várzea* forests the species are gradually substituted during the period of forest succession
436 and with the decrease of the influence of flooding (Worbes et al. 1992; Wittmann et al. 2004).

437 Due to the substitution of species in gradients, we found indicator species of specific
438 environmental conditions. On the other hand, the majorities of species (~77 % of the common
439 species) are capable of being distributed along the whole gradient, and are able to be
440 characterized as oligarchic species (*sensu* Pitman et al. 2001). Our data indicate that there exist
441 a number of species in the forest for which it is possible to realize prediction with respect to
442 their role in the structuring of communities. The predictions are possible, since some species are
443 common and occur indiscriminately characterizing a oligarchy species (Pitman et al. 2001), and
444 some are indicator species for specific habitats.

445 Among the VA indicator species we found species that occur both in the flooded forests and the
446 upland forests (Wittmann et al. 2006). Among examples we can cite, *Hura crepitans*, *Virola*
447 *surinamensis* and *Himatanthus sucuuba*. *H. crepitans* have ample distributions that extend as
448 well to the dry tropical forests of Central America. *V. surinamensis* has a distribution in upland
449 forests in the Amazon, often associated with riparian habitats. *H. sucuuba*, despite occurring in
450 upland forests, is a species that presents physiological modifications, depending on the habitat
451 in which its population is found (Ferreira et al. 2007). Seeds and plants of *H. sucuuba*
452 originating in upland habitats do not possess the same “fitness” as when in flooded habitats
453 (Ferreira et al. 2007). Other VA indicator species possess distributions more associated with
454 seasonally flooded forests. Such is the case of *Maquira coriacea*, which can be found with
455 densities superior to 14 ind*ha⁻¹ in the lesser flooded areas of the *várzea* forests of the Ucayali
456 River in Peru (Nebel et al. 2001b).

457 For VB, we found three indicator species for the group of species with a density of ≥ 5 ind*ha⁻¹,
458 being that two are strongly associated with locations that have extreme flooding depths.

459 *Pseudobombax munguba* is a species known for colonizing the secondary stages of succession
460 in the VB forests of the Central Amazon (Worbes et al. 1992). This species possesses small

461 seeds that are dispersed by the wind and water during the rainy season (Parolin et al. 2004).
462 Another marked characteristic of this species is its capacity to store water in its trunk and lose
463 its leaves during the flooding, which makes possible a reduction in energetic metabolism
464 (Parolin et al. 2004).
465 The lower number of VB indicator species is expected to be related to the fact that these species
466 frequently occur as well in VA areas. This fact does not happen with the VA indicator species.
467 This observation suggests that the restrictions on the species along the flooding gradient are not
468 the same. In the locations of lesser flooding (VA), the effect of flooding on the reduction of the
469 capacity to colonize the environment is expected to be less restrictive towards the species. In the
470 locations of greater flooding (VB), the species are expected to suffer greater environmental
471 restriction and competition. In addition to more species being capable of colonizing the VA
472 areas, we also observed the presence of sub-forest species and emerging species among the
473 indicators of these environments. These species contributed considerably to the increase of the
474 diversity.
475 We observed that the *várzea* forests are rather heterogeneous in species composition and that
476 the complex environmental gradient occasioned by the flooding pulse is the factor that most
477 influences the distribution of diversity in these forests. The narrow relation between the
478 diversity and composition of trees and the environmental gradient of flooding depth needs to be
479 used for more precise comparisons between *várzea* forests from different locations, landscapes,
480 and regions. The description of this pattern can improve the understanding of the distribution of
481 diversity and of the species of trees in flooded tropical forests, contributing to the formulation
482 of conservation strategies of these forests.

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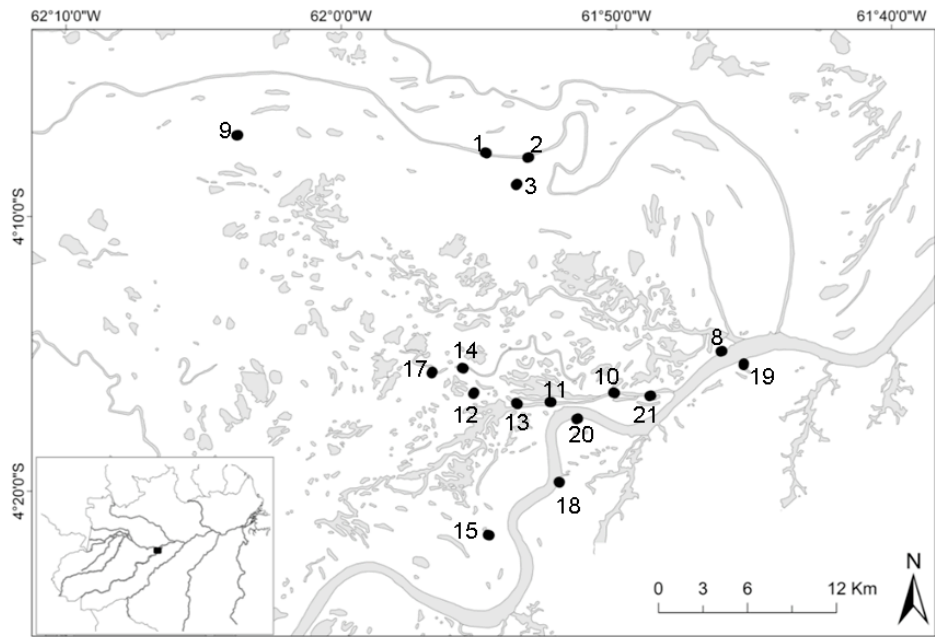
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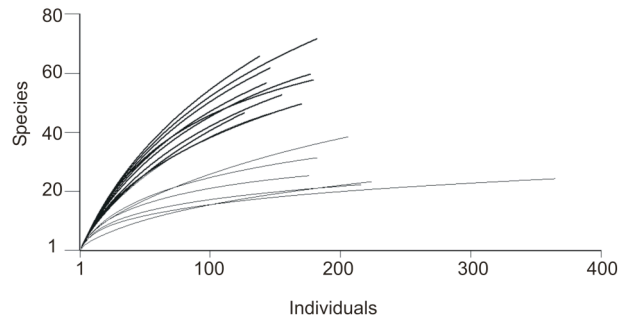
619 **Figures e Tables**



620

621 **Figure 1:** Flooding landscape of the lower Purus River, Central Amazon, Brazil. The dark
622 circles and numbers represent the locations of the sampled plots. The figure in the lower left
623 corner indicates the location of the studied landscape in relation to the Amazon Basin.

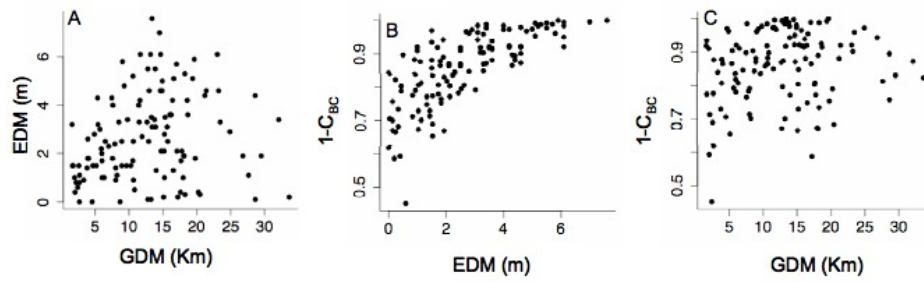
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625 **Figure 2:** Species accumulation curves for the 16 inventory plots in the *várzea* forests of the
626 low Purus river in RDS-PP. Curves with lines in black correspond to the plots: 2, 9, 18, 1, 3, 19,
627 21, 10, 8 and 15, respectively, from top to bottom.

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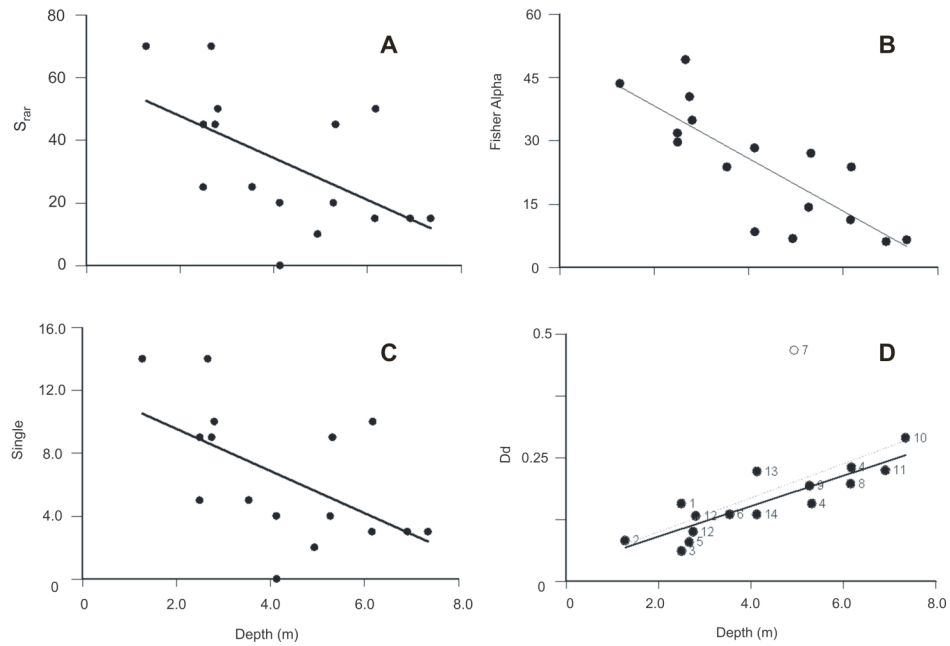
629 **Figure 3:** Dispersion graphs for the distance matrixes between the pairs of plots. A)

630 Environmental Distance Matrix EDM in meters of flooding depth and geographical distance

631 matrix GDM in kilometers between pairs of plots; B) Values of floristic dissimilarity (1-C_{BC}) in

632 relation to the EDM; C) Values of floristic dissimilarity (1-C_{BC}) in relation to GDM.

633



633

634 **Figure 4:** Graphs of the flooding depth gradient (m) in relation to A) Species richness

635 rarefacted in 100 individuals; B) α Fisher's Alfa coeficient; C) Singletons – number of species

636 with one individual in the landscape (5ha); D) D_d – Berger-Parker Index, where: 1 - *Maquira*

637 *coriacea*; 2 - *Hura crepitans*; 3 - *Pterocarpus amazonum*; 4 - *Mabea taquari*; 5 - *Garcinia*

638 *madruno*; 6 - *Triplaris surinamensis*; 7 *Luehea cymulosa*; 8 - *Guatteria cf. olivacea*; 9 -

639 *Tabebuia barbata*; 10 - *Pseudobombax munguba*; 11 - *Pouteria elegans*; 12 - *Virola*

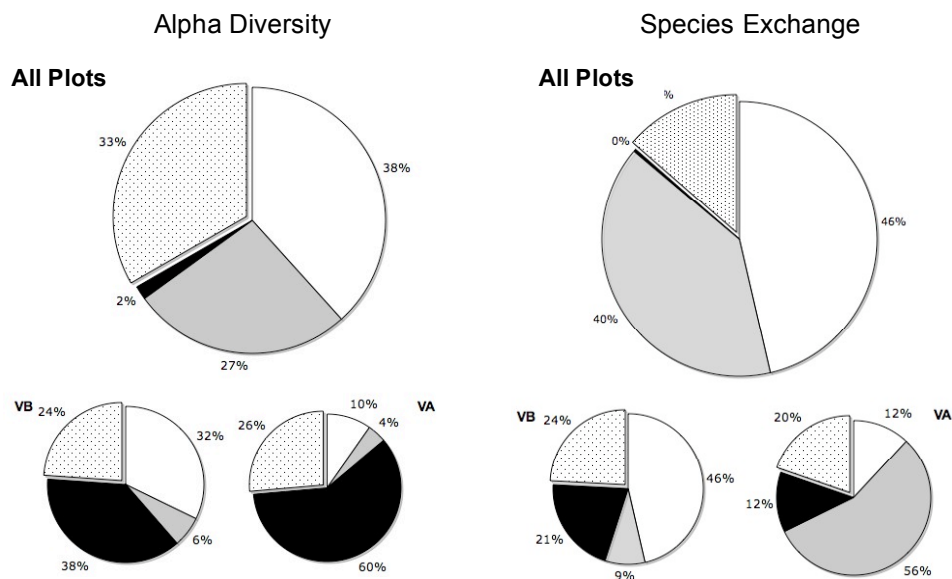
640 *surinamensis*; 13 - *Leonia glycyarpa*; 14 - *Hevea spruceana*; solid line: estimated straight line

641 without residual value (hollow point in the graph): dotted line: estimated straight line with

642 residual value. Corresponding values for the plots with 3 125 m² allocated in the *várzea* forests

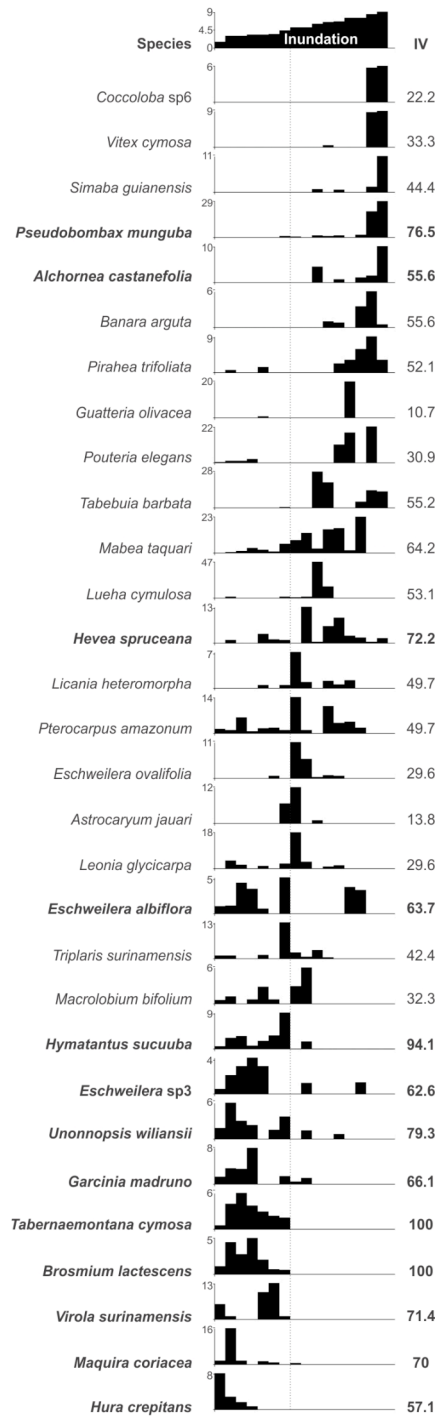
643 of the lower Purus River.

644



645 **Figure 5:** Partition of the variation of the multiple linear model predictive of the Fisher alpha
 646 diversity and of the species exchange represented in the NMDS axis for the matrix of floristic
 647 dissimilarity ($1-C_{BC}$). Following clockwise: **White** = environmental explanation only; **Gray** =
 648 geographical and environmental space explanation; **Black** = geographical space explanation;
 649 **Dotted** = not explained by the model; percentages relative to the total variation of the model
 650 (r^2). The total utilizes the information from the 16 sampled locations; VB only the information
 651 from the lower *várzea* (flooding depth < 3 m, n = 9); VA only for the group from the upper
 652 *várzea* (flooding depth \geq 3 m, n = 7).

653



653

654 **Figure 6:** Direct ordering of the common species with a density of $\geq 5 \text{ ind*ha}^{-1}$ in relation to
 655 the flooding depth gradient, Indicator Values (IV) and associated probability; values in bold
 656 show the species with a significant IV value ($p < 0.05$). The dark bars in the figure indicate the
 657 relative abundance of the species in the plots along the flooding depth gradient, the upper
 658 diagram represents the inundation in the 16 plots sampled, the locations with the lower depth on
 659 the left, and locations with greater flooding depth on the right; the dotted line separates the plots
 660 from the upper várzea ($< 5 \text{ m}$) and from the lower várzea ($\geq 5 \text{ m}$).

661 **Table 1:** Environmental and structural attributes of the plots (0.3125 ha) from the inventory in
662 the *várzea* forests of the RDS-PP. Depth (m) (min - max) - Average depth (m) and maximum
663 and minimum values (n=15) and *HD historical depth, which is corrected by -1.8 m the
664 maximum historical average level reach in the Purus river in 28 years; N - Abundance in
665 number of individuals; AB_t - Total Basal Area (m²); S_{obs} - Observed species richness; Single –
666 Singletons, the number of species represented by one individual in the landscape; α Fisher (SD)
667 - Fisher's Alpha coefficient (standard deviation); Dd - Index of Berger-Parker. Below are the
668 values for the sum of the plots. The values are for plots of 3 125 m².

Plot	Depth (m) (min - max); *HD (m)	N	AB _t (m ²)	S _{obs}	α Fisher (SD)	Single	Dd
1	3.1 (3.1 - 3.2);1.3*	178	15.2	60	31.8 (3.7)	5	0.16
2	1.6 (1.3 - 2.2);0.0*	183	10.0	73	43.5 (5.17)	14	0.08
3	3.1 (2.3 - 3.7);1.3*	180	9.8	58	29.6 (3.5)	9	0.06
8	6.6 (5.7 - 7.1);4.8*	127	8.8	47	26.9 (3.8)	9	0.16
9	3.3 (3.0 - 3.8);1.5*	139	8.4	66	49.1 (6.9)	14	0.08
10	4.4 (4.0 - 4.8); 2.6*	171	10.2	50	23.77 (2.8)	5	0.13
11	6.1 (5.7 - 6.9); 4.3*	225	11.4	24	6.8 (0.8)	2	0.47
12	7.7 (7.4 - 7.9); 5.9*	183	9.9	32	11.2 (1.3)	3	0.20
13	6.5 (6.2 - 7.0); 4.7*	207	12.3	39	14.2 (1.6)	4	0.19
14	9.1 (9.0 - 9.5); 7.3*	217	14.2	23	6.5 (0.8)	3	0.29
15	7.7 (7.1 - 8.1); 5.9*	148	8.9	47	23.76 (3.0)	10	0.23
17	8.6 (8.4 - 8.9); 6.8*	366	15.2	25	6.1 (0.6)	3	0.22
18	3.4 (2.9 - 3.7); 1.6*	150	10.3	62	40.4 (5.4)	9	0.10
19	3.5 (3.3 - 4.2); 1.7*	144	7.6	57	34.85 (4.6)	10	0.13
20	5.1 (4.9 - 5.8); 3.3*	177	14.9	26	8.4 (1.0)	0	0.22
21	5.1 (4.8 - 5.5); 3.3*	156	8.5	53	28.3 (3.6)	4	0.13
Total	-	2951	175.78	304	85.02 (5.71)	104	-

669 **Table 2:** Results of the simple linear regression models for the structural attributes of the plots
670 in *várzea* forest in the RDS-PP. S_{rar} - Species Richness rarefy in 100 individuals; α Fisher –
671 Fisher’s alpha coefficient; Single- Singletons, number of species with one individual in the
672 landscape; Dd - Berger-Parker Equitability Index; N - Abundance; and ABt - Total Basal Area.
673 HD - maximum historical average flooding depth in the plot; EP - Standard Error of the model
674 and parameters. Data for plots with 3 125m²; * p<0.05; ** p<0.01; ⁽¹⁾ estimated model without
675 outlier.

Model	A (± EP)	B (± EP)	B_{std}	r²	r²_{std}	EP
$S_{rar} = A + B * HD \pm EP$	53.5 (3.9)	-4.8 (0.9)**	-0.80	0.64	0.61	8.33
α Fisher = A + B * HD ± EP	42.5 (4.1)	-5.16 (1.0)**	-0.80	0.65	0.62	8.65
Single = A + B * HD ± EP	10.2 (1.7)	-1.0 (0.4)*	-0.56	0.31	0.26	3.65
Dd = A + B * HD ± EP	0.07 (0.06)	0.02 (0.009)**	0.62	0.38	0.34	0.08
⁽¹⁾ Dd = A + B * HD ± EP	0.07 (0.01)	0.02 (0.004)**	0.87	0.75	0.74	0.03

676

676 **Table 3:** Pearson coefficient values (r) for the correlations between the matrix of floristic
 677 dissimilarity (1- C_{BC}) and the matrixes of environmental distance (flooding depth) and
 678 geographical distance. **Total** utilizes the total with the 16 plots; **VB** utilizes only the lower
 679 *várzea* plots (n=9); **VA** utilizes only the upper *várzea* (n = 7); ** p < 0.01 in Mantel procedure
 680 10 000 permutations.

Correlation	Total	VB	VA
1- C _{BC} vs Environmental	0.73**	0.53 **	0.39
1- C _{BC} vs Geographical	0.17	0.16	0.26
Geographical vs Environmental	0.20	0.20	-0.20

681

681 **Table 4:** Values of the *b* coefficient standardized form the explanatory variables: HD -
682 maximum historical average level of flooding depth; Lat – latitude; Long - longitude of the
683 multiple linear models for the Fisher alpha diversity (Fisher α diversity) and for the 1st NMDS
684 axis of the matrix of floristic dissimilarity (1-C_{BC}) (Species Exchange). **Total** utilizes the total
685 with the 16 plots; **VB** utilizes only the lower *várzea* plots (n=9); **VA** utilizes only the upper
686 *várzea* (n = 7). **F** sum of the square of total residuals; **r²** global adjustment of the model; **r²_{std}**
687 standardized adjustment of the model; **p** probability associated with the model. * p < 0.05 e **
688 p<0.01 for the values of the estimated *b* coefficient.

689

Mo								
del		HD	Lat	Long	F	r²	r²_{std}	p
Fisher α Diversity	Total	-0.848**	-0.047	-0.144	7.979	0.66	0.58	0.003
	VB	0.462	-0.539	1.134*	4.643	0.73	0.58	0.066
	VA	-0.768*	-0.688	-0.873*	2.652	0.73	0.45	0.222
Species Exchange	Total	-0.934**	-0.02	0.055	25.547	0.86	0.83	<0.001
	VB	-0.515	-0.345	0.407	6.778	0.8	0.68	0.033
	VA	0.944*	0.39	-0.239	2.436	0.71	0.42	0.242

Conclusão Geral

Observamos que as florestas de várzea são bastante heterogêneas em composição de espécies e que o gradiente ambiental complexo ocasionado pelo pulso de inundação é o fator que mais influencia na distribuição da diversidade dessas florestas. A estreita relação entre a diversidade e composição de árvores e o gradiente ambiental de profundidade de inundação necessita ser utilizada para comparações mais precisas entre florestas de várzea de diferentes localidades, paisagens e regiões. A descrição deste padrão pode melhorar o entendimento da distribuição da diversidade e das espécies de árvores nas florestas tropicais inundáveis, contribuindo para formulações de estratégias de conservação dessas florestas.

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Apêndice

Fichas de avaliação e parecer dos revisores do projeto de mestrado, aula de qualificação, dissertação de mestrado e a ata da defesa pública.



Ministério da
Ciência e Tecnologia



Avaliação de projeto de mestrado

Título: **A estrutura da floresta de várzea do baixo Purús e sua relação com a duração da inundação**
Aluno(a): **BRUNO GARCIA LUIZE**
Orientador(a): **Eduardo Martins Venticinqu**

Avaliador(a): **Bruce Walker Nelson**

Devem ser considerados os seguintes pontos principais:

- A revisão de literatura é suficientemente completa?
- O projeto tem potencial para pelo menos uma publicação em periódico científico indexado?
- Os objetivos e a metodologia indicam que o aluno tem base científica suficiente para executar a proposta?
- O projeto é factível no tempo disponível para um mestrado (24 meses)?
- Os recursos financeiros e logísticos são adequados para a execução da proposta?

Parecer:

- Aprovado
- Aprovado com correções (não necessita reavaliação)*
- Necessita revisão (deve retornar ao avaliador para reavaliação)*
- Necessita revisão (deve retornar ao conselho de curso para avaliação do cumprimento das recomendações do avaliador)*
- Reprovado

Envia ficha de avaliação com cópia anotada do projeto sem cópia anotada do projeto

Manaus, 27 de outubro de 2008

assinatura do avaliador(a)



Ministério da
Ciência e Tecnologia



Avaliação de projeto de mestrado

Título: **A estrutura da floresta de várzea do baixo Purús e sua relação com a duração da inundação**

Aluno(a): **BRUNO GARCIA LUIZE**

Orientador(a): **Eduardo Martins Venticinque**

Avaliador(a): **Leandro Valle Ferreira**

Devem ser considerados os seguintes pontos principais:

- A revisão de literatura é suficientemente completa?
- O projeto tem potencial para pelo menos uma publicação em periódico científico indexado?
- Os objetivos e a metodologia indicam que o aluno tem base científica suficiente para executar a proposta?
- O projeto é factível no tempo disponível para um mestrado (24 meses)?
- Os recursos financeiros e logísticos são adequados para a execução da proposta?

Parecer:

Aprovado

Aprovado com correções (não necessita reavaliação)

Necessita revisão (deve retornar ao avaliador para reavaliação)

Necessita revisão (deve retornar ao conselho de curso para avaliação do cumprimento das recomendações do avaliador)

Reprovado

Envia ficha de avaliação com cópia anotada do projeto sem cópia anotada do projeto

BELÉM, PARA , 3 de NOVEMBRO de 2008

_____ assinatura do avaliador(a)



Ministério da
Ciência e Tecnologia



M

Avaliação de projeto de mestrado

Título: **A estrutura da floresta de várzea do baixo Purús e sua relação com a duração da inundação**

Aluno(a): **BRUNO GARCIA LUIZE**

Orientador(a): **Eduardo Martins Venticinqu**

Avaliador(a): **Maria Teresa Fernández Piedade**

Devem ser considerados os seguintes pontos principais:

→ A revisão de literatura é suficientemente completa?

Sim, em termos gerais.

→ O projeto tem potencial para pelo menos uma publicação em periódico científico indexado?

SIM

→ Os objetivos e a metodologia indicam que o aluno tem base científica suficiente para executar a proposta?

Parcialmente – Considerar os comentários ao longo do texto

→ O projeto é factível no tempo disponível para um mestrado (24 meses)?

Sim, com trabalho intensivo no campo. Problemas taxonômicos podem ser fortemente limitantes.

→ Os recursos financeiros e logísticos são adequados para a execução da proposta?

O Projeto não apresenta cronograma financeiro. O cronograma de atividades é confuso. Há vários campos coloridos codificados. Sem, contudo, informar o que significam as letras e as cores. RECOMENDO ATENÇÃO DO CONSELHO PARA ESTES ASPECTOS REFERENTES AOS CRONOGRAMAS.

Parecer:

() Aprovado

(X) Aprovado com correções (não necessita reavaliação)

() Necessita revisão (deve retornar ao avaliador para reavaliação)

() Necessita revisão (deve retornar ao conselho de curso para avaliação do cumprimento das recomendações do avaliador)

() Reprovado

Envia ficha de avaliação (X) com cópia anotada do projeto () sem cópia anotada do projeto

Manaus, 30 de outubro de 2008

Maria Teresa F. Piedade
assinatura do avaliador(a)

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): BRUNO GARCIA LUIZE
 Curso: ECOLOGIA
 Nível: MESTRADO
 Orientador(a): EDUARDO MARTINS VENTICINQUE

Título:

"A ESTRUTURA DA FLORESTA DE VÁRZEA DO BAIXO PURÚS E SUA RELAÇÃO COM A INUNDAÇÃO

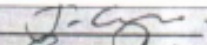
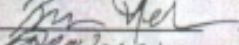
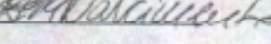
BANCA JULGADORA

TITULARES:

José Luis Camargo (INPA/PDBFF)
 Bruce Nelson (INPA)
 Henrique Nascimento (INPA)

SUPLENTE:

Flávia Costa (INPA)
 Bruce Forsberg (INPA)

EXAMINADORES	PARECER	ASSINATURA
José Luis Camargo (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Bruce Nelson (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Henrique Nascimento (INPA/PDBFF)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Flávia Costa (INPA)	() Aprovado () Reprovado	_____
Bruce Forsberg (INPA)	() Aprovado () Reprovado	_____

Manaus(AM), 26 de janeiro de 2009

OBS: _____

Avaliação de dissertação de mestrado

Título: **A estrutura da floresta de várzea do baixo Purus e sua relação com a duração da inundação**

Aluno: **BRUNO GARCIA LUIZE**

Orientador: **Eduardo Martins Venticinque**

Co-orientador: -----

Avaliador: **Ana Luisa Kerti Mangabeira Albernaz**

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	()	(x)	()	()
Revisão bibliográfica	()	(x)	()	()
Desenho amostral/experimental	(x)	()	()	()
Metodologia	(x)	()	()	()
Resultados	(x)	()	()	()
Discussão e conclusões	()	()	(x)	()
Formatação e estilo texto	()	(x)	()	()
Potencial para publicação em periódico(s) indexado(s)	()	()	(x)	()

PARECER FINAL

Aprovada

Aprovada com correções (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

Necessita revisão (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

Reprovada (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Belém
Local

, 19 de maio de 2010
Data

Ana Luisa Kerti Albernaz
Assinatura

Avaliação de dissertação de mestrado

Título: A estrutura da floresta de várzea do baixo Purus e sua relação com a duração da inundação
 Aluno: BRUNO GARCIA LUIZE
 Orientador: Eduardo Martins Venticinque Co-orientador: ----

Avaliador: Ary Oliveira Filho (ICB-UFMG)

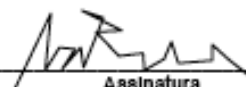
Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(X)	()	()	()
Revisão bibliográfica	(X)	()	()	()
Desenho amostral/experimental	(X)	()	()	()
Metodologia	()	(X)	()	()
Resultados	(X)	()	()	()
Discussão e conclusões	(X)	()	()	()
Formatação e estilo texto	()	()	(X)	()
Potencial para publicação em periódico(s) Indexado(s)	(X)	()	()	()

PARECER FINAL

- () Aprovada
 (X) Aprovada com correções (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)
 () Necessita revisão (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)
 () Reprovada (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Belo Horizonte, 22 de maio de 2010,
 Local Data



Assinatura

Comentários e Sugestões

Trata-se de um trabalho de grande relevância científica e para a conservação. O autor fez uso de um desenho de amostragem excelente e de análises de ponta, além de se mostrar inteirado sobre os modelos teóricos sobre a estruturação de comunidades arbóreas tropicais. Parabéns a aluno e orientador. Fiz correções de forma ao longo de todo o texto, pois há muitos erros ortográficos, de pontuação e concordância, em português e inglês, mas que não comprometem a excelência do trabalho. Apenas exigem correções. Tenho dúvidas sobre a compatibilidade entre abordagens paramétricas e não paramétricas combinadas nas correlações (veja página 15). Sugiro consultar um (bom) estatístico antes de submeter, mas, caso haja mesmo restrições, não alterar para a defesa final.

Avaliação de dissertação de mestrado

Título: **A estrutura da floresta de várzea do baixo Purus e sua relação com a duração da inundação**

Aluno: **BRUNO GARCIA LUIZE**

Orientador: **Eduardo Martins Venticinqu**

Co-orientador: -----

Avaliador: Pia Parolin

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	()	()	()
Revisão bibliográfica	(x)	()	()	()
Desenho amostral/experimental	(x)	()	()	()
Metodologia	(x)	()	()	()
Resultados	(x)	()	()	()
Discussão e conclusões	(x)	()	()	()
Formatação e estilo texto	()	(x)	()	()
Potencial para publicação em periódico(s) indexado(s)	()	(x)	()	()

PARECER FINAL

Aprovada

Aprovada com correções (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

Necessita revisão (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

Reprovada (indica que o trabalho não tem o nível de qualidade adequado para uma tese)



_____ Hamburgo _____, 19.5.2010
Local Data

Assinatura

Comentários e sugestões

Acho que a tese é interessante, ela trata de um tema "up to date" com uma base de dados muito boa, está bem escrita e bem analisada. O contexto de discussão é bom. Acho que deveria juntar o aspecto de plantas generalistas vs. especialistas, sendo as generalistas distribuídas em amplos espaços. Cuidado com a ortografia: tem muitos erros no abstract inglês e na maneira de escrever os nomes de autores e os nomes botânicos latinos de plantas. Coloquei algumas correções no texto.



ATA DA DEFESA PÚBLICA DA
DISSERTAÇÃO DE MESTRADO DO
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA DO INSTITUTO NACIONAL DE
PESQUISAS DA AMAZÔNIA.

Aos 29 dias do mês de junho do ano de 2010, às 14:30 horas, na sala de aula do Programa de Pós-Graduação em Ecologia PPG-ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: **Dr. Alberto Vicentini**, do Instituto Nacional de Pesquisas da Amazônia, **Dr. Jochen Schongart**, do Instituto Nacional de Pesquisas da Amazônia, **Dra. Veridiana Vizoni Scudeller**, da Universidade Federal do Amazonas, tendo como suplentes o Dr. Antônio Carlos Webber, da Universidade Federal do Amazonas, e o Dr. José Júlio de Toledo, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública da **DISSERTAÇÃO DE MESTRADO** de **BRUNO GARCIA LUIZE**, intitulada "A estrutura da floresta de várzea do baixo Purus e sua relação com a duração da inundação", orientado pelo Dr. Eduardo Martins Venticinquê, da Universidade Federal do Amazonas.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

- APROVADO(A) REPROVADO(A)
 POR UNANIMIDADE POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Dr(a). Alberto Vicentini

Dr(a). Jochen Schongart

Dr(a). Veridiana Vizoni Scudeller

Coordenação do PPG-ECO/INPA
CLAUDIA KELLER

Coordenação de Capacitação do INPA

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