1   *Title*: Biomass and demographic dynamics of the Brazil-nut family (Lecythidaceae) in a mature
2   Central Amazon rain forest
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8   * Deceased
9   *Keywords*: biomass, growth, mortality, recruitment, habitat associations, flood disturbance
10 *Highlights*:
11 • The number of Lecythidaceae individuals decreased by >1000, but basal area and
12   biomass did not change significantly over 30 years.
13 • Mortality is highest in the lower-lying, wetter habitats.
14 • The most abundant species in the plot do not overlap in their habitat associations, nor do
15   sister species.
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17

18 *Abstract*

19   In this study, we analyze the demographic rates and biomass dynamics of Lecythidaceae

20 in a 100-ha permanent forest plot in the Central Amazon. We characterize habitats in the plot,

21 analyze the effect of habitat on tree density, species richness, and biomass and demographic

22 dynamics, and quantify significant species habitat associations. The plot experienced a 13.2 %

23 net loss of Lecythidaceae individuals (n = 1023) but aboveground biomass (AGB; Mg ha^{-1}) did

24 not differ between the two censuses. Growth rates averaged 1.2 mm year^{-1} with high intraspecific

25 variation and differed significantly among species height classes. Stem density and species

26 richness decreased in all six *terra firme* habitats and were significantly lower in both years in the

27 flood disturbed habitat. Only the flood disturbed areas experienced a significant loss in AGB,

28 along with the highest annual mortality, recruitment, and growth rates across the plot. The lower-

29 lying habitats experienced higher mortality rates than the slopes and plateaus, suggesting too

30 much moisture is a higher risk to Lecythidaceae individuals than drought in this plot. There were

31 no overlapping habitat associations among sister species, or among the seven most abundant

32 species, which suggests that *terra firme* habitat association provides a niche partitioning

33 mechanism for closely related Lecythidaceae species. As intended with its establishment, this

34 plot continues to provide integral baseline data for of one of the most ecologically dominant and

35 culturally significant tree families in the Amazon region.

36 ***Introduction***

37   Long term research on the demography and biomass dynamics of tropical tree species,

38 and on how these dynamics relate to environmental conditions, is critical to predict how tropical

39 forests will respond to global change. Such data are also needed to sustainably manage these

40 forests for forest products and biodiversity conservation (Davies et al., 2021). Baseline data for

41 trees in the Amazon basin is particularly important considering recent land use and climate

42 changes, combined with the region's outsize role in global carbon budgets (Laurance et al., 2000;

43 Longo et al., 2016). In permanent forest inventory plots tagged and geo-located trees provide

44 ecological information about demographic rates, life stage transitions (Pinero et al., 1984),

45 phenology (Lepsch-Cunha and Mori, 1999a), spatial dynamics, and responses to extreme

46 weather events (Feldpausch et al., 2016; Mori and Becker, 1991), among other processes. Forest

47 inventory plots can illuminate ecological processes that underlie forest composition and

48 dynamics at local scales (Zuleta et al., 2017), while providing opportunities for in depth studies

49 of focal clades (Baker et al., 2017; Lepsch-Cunha and Mori, 1999b; Mori and Lepsch-Cunha,

50 1995).

51   The Lecythidaceae family (Order Ericales) has considerable economic, cultural, and

52 ecological significance in the Amazon basin (Da Cunha and De Albuquerque, 2006; Mori and

53 Prance, 1990; Perreault, 2005; Prance et al., 1987) and is emblematic of old growth Amazon rain

54 forest (Guevara et al., 2017; Pitman et al., 2008; ter Steege et al., 2013). The Central Amazon has

55   particularly high Lecythidaceae diversity, resulting from a combination of higher endemism than

56   other regions and migration from other areas (Mori et al., 2016). Lecythidaceae ranks third in

57   family-level abundance in Amazon forests (following Fabaceae and Sapotaceae); it contains one

58   of the most abundant Amazon tree genera, *Eschweilera*, and one of Amazonia's most widespread

59   and abundant species, *Eschweilera coriacea* (Duque et al., 2017; ter Steege et al., 2020). The

60   family has a disproportionately high number of hyperdominant species given its richness (ter

61   Steege et al., 2013). Lecythidaceae are dominant among a variety of forest strata, and *E. coriacea*

62   is the only species to be hyperdominant in all size categories and in all regions of the Amazon

63   (Draper et al., 2021). Four Lecythidaceae species are in the top 20 species contributing to

64   biomass in lowland Amazonia, including two of the top three – *E. coriacea* and the Brazil nut

65   tree *Bertholletia excelsa* (Fauset et al., 2015). Because of its contribution to biomass,

66   Lecythidaceae is important in global biogeochemical processes such as carbon sequestration.

67   In the past several decades, the Amazon is thought to have acted as a carbon sink, with

68   aboveground biomass (AGB) of trees ≥10cm DBH (diameter at breast high) increasing in mature

69   forest (Baker et al., 2004a; De Castilho et al., 2010; Phillips et al., 1998). Additionally, large-

70   stature, fast-growing trees, including two Lecythidaceae genera, *Eschweilera* and *Corythophora*,

71   have increased in density in some studies (Laurence et al. 2004). Many large-scale analyses

72   using networks of permanent plots and averaging across all clades have concluded that AGB is,

73   on average, increasing in the Amazon basin (Phillips and Lewis 2014; but see Wright 2005).

74   Information on how particular clades change in biomass, and what factors influence those

75   dynamics at the species level, is less well reported. For clades that have such an outsize

76   contribution to Amazon biomass dynamics, however, taxon-specific information can be

77   informative for conservation decisions and management.

78 Habitat factors may strongly influence demography and biomass dynamics at the species

79 level. Species may be associated with favored habitats based on physiological traits and

80 tolerances. An example is topographically influenced hydrologic variation (Zuleta et al., 2020),

81 which is one way in which species partition niche space, and may therefore contribute to

82 coexistence of closely related species (Harms et al., 2001). Species may be competitively

83 dominant and therefore more relatively abundant if they are better able to perform in certain

84 conditions (Harms et al., 2001). Habitat associations are known to change with life stage (Comita

85 et al., 2007), and demographic performance may not align particularly well with distribution-

86 based habitat associations (Bin et al., 2016; Kenfack et al., 2014). This suggests that adult habitat

87 associations may not be stable, although the extent of their dynamism remains unclear.

88 Differences in dynamism are well documented at the Amazon-wide scale as a function of climate

89 and edaphic conditions (Phillips et al., 2004; Quesada et al., 2009). At the local scale, if certain

90 species, particularly those with higher wood density, are associated with habitats that are

91 changing due to precipitation and drought variation in the Amazon, an overall change in biomass

92 trends may occur.

93 Small-scale disturbance can also play a significant role in forest dynamics (Negrón-

94 Juárez et al 2018). In *terra firme* forest, blow-downs (Negrón-Juárez et al., 2010; Nelson et al.,

95 1994), lightning (Gora et al., 2020), and anomalous weather events (Mori and Becker, 1991) can

96 influence forest dynamics by increasing mortality and creating gaps which increase available

97 light. Flooding plays a large role in structuring tropical *várzea* and *igapó* forest, which are

98 defined by predictable annual flood pulses that filter species adapted to tolerate anoxic

99 conditions (Parolin et al., 2004). Flood disturbance in *terra firme* is uncommon, but standing

100 water in *terra firme* depressions has been documented (Kahn, 1987; Mori and Becker, 1991;

101 Myster, 2007; Rossano Mendes Pontes et al., 2012). The extent to which *terra firme* flooding

102 influences forest demographic and biomass dynamics remains an open question.

103   In this paper, we report on the dynamics of Lecythidaceae a large (100-hectare)

104 permanent forest plot north of Manaus, Brazil in which all individuals in the family were first

105 studied in the late 1980s and recensused for this study after 30 years. We analyze the effect of

106 species, tree size, and height class on demographic rates. Additionally, we characterize habitats

107 in the plot, and analyze the effect of habitat on tree density, species richness, and biomass and

108 demographic dynamics. We quantify significant species habitat associations, and determine

109 whether they have remained stable over the past 30 years.

110 **Methods:**

111 *Study Site and plot:*

112   The study site is part of the Biological Dynamics of Forest Fragments Project (BDFFP),

113 located approximately 70 km north of Manaus, Brazil. The 100-ha Lecythidaceae plot is located

114 in continuous forest Reserve 1501, or "KM 41", which is located on *terra firme*, well-drained

115 Tertiary sediments with primarily clayey latosols (oxisols), that are poor in nutrients (Fearnside

116 and Filho, 2001; Mori et al., 2001). Mean annual temperature is 26.7° C, and mean annual

117 rainfall is 2325mm, with a dry season from July to September generally with less than 100mm of

118 rainfall (Bierregaard et al., 2001). Low-lying areas within the plot accumulate standing water

119 during years of unusually heavy precipitation; a flood was recorded in 1989, when >1m of

120 standing water was observed in 7 areas of the plot (Mori and Becker, 1991).

121   The Lecythidaceae plot was established to study the ecology and systematics of an

122 important Central Amazon tree clade, and to obtain precise baseline information on frequency,

123 density, dominance, and species richness that could be used to compare changes in composition

124 and demography as a result of climate change and forest fragmentation (Mori et al., 2001). All

125 Lecythidaceae individuals ≥10 cm DBH were identified, measured, tagged, and mapped, and

126 vouchers were collected for each species and for any individual for which the determination was

127 uncertain. Detailed taxonomic work has been done on all species in the plot (Mori and Lepsch-

128 Cunha, 1995), therefore identification errors are likely to be uncommon compared to other

129 locations.

130   Mori and colleagues recorded 38 species of Lecythidaceae in the initial census of the

131 100-ha plot. The most abundant species in the plot was the hyperdominant *Eschweilera coriacea*,

132 followed by *E. truncata*. The rarest species was the Brazil nut tree *Bertholletia excelsa*, which

133 was represented by a single individual. Eight genera are represented in the plot (*Allantoma,*

134 *Bertholletia, Cariniana, Corythophora, Couratari, Eschweilera, Gustavia*, and *Lecythis*),

135 although *Eschweilera* and *Lecythis* are non-monophyletic (Mori et al., 2007). All species were

136 assigned to one of three adult height classes by Mori & Lepsch Cunha (1995) determined by

137 species maximum height at maturity: understory, which we will refer to as subcanopy (≤25m),

138 canopy (25-35m), and emergent (>35m).

139 ***2018-2019 Census and taxonomic determinations:***

140   We performed a complete recensus of the Lecythidaceae plot between February 2018 and

141 March 2019. We attempted to locate all tagged Lecythidaceae trees from the original census, and

142 DBH was measured at 1.3 or above buttresses. Trees were recorded as missing if their tags could

143 not be found, unless a conspecific tree lacking a tag and with DBH equal to or larger than the

144 missing tree was found in the same location (x, y coordinates of the 20x20 plot), in which case it

145 was assumed to be the missing individual.

146   When a tree new to the 10cm size class was found, this recruit was identified, tagged, its

147   DBH was measured, and the tree was mapped by measuring the distance and the angle from the
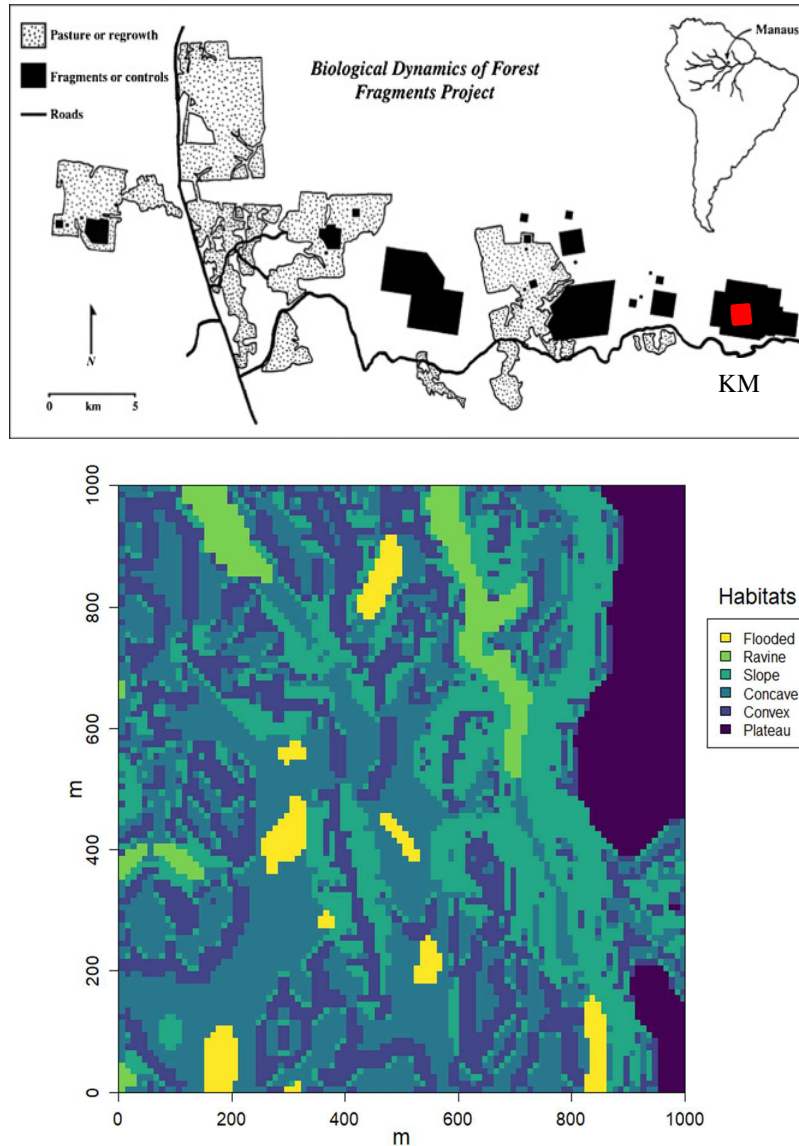
Fig. 1: Top: map of the BDFFP, modified from Laurance et al. 2011. Red square shows approximate location of the "KM 41" Lecythidaceae plot. Bottom: map of the 6 habitats in the Lecythidaceae plot.

148   nearest 20x20m quadrat corner post. If a recruit could not be identified in the field, an herbarium

149   specimen was made and deposited at BDFFP for subsequent verification. Fertile specimens were

150   deposited at the INPA (Instituto Nacional de Pesquisas da Amazônia) herbarium.

151   Eighty individuals in the plot were sampled for DNA for studies on hybridization (Larson

152   et al., 2021) and systematics (Vargas et al., in prep) of Lecythidaceae. The taxonomic

153   identification of eleven individuals in the plot, including three recruits (13.8% of the total
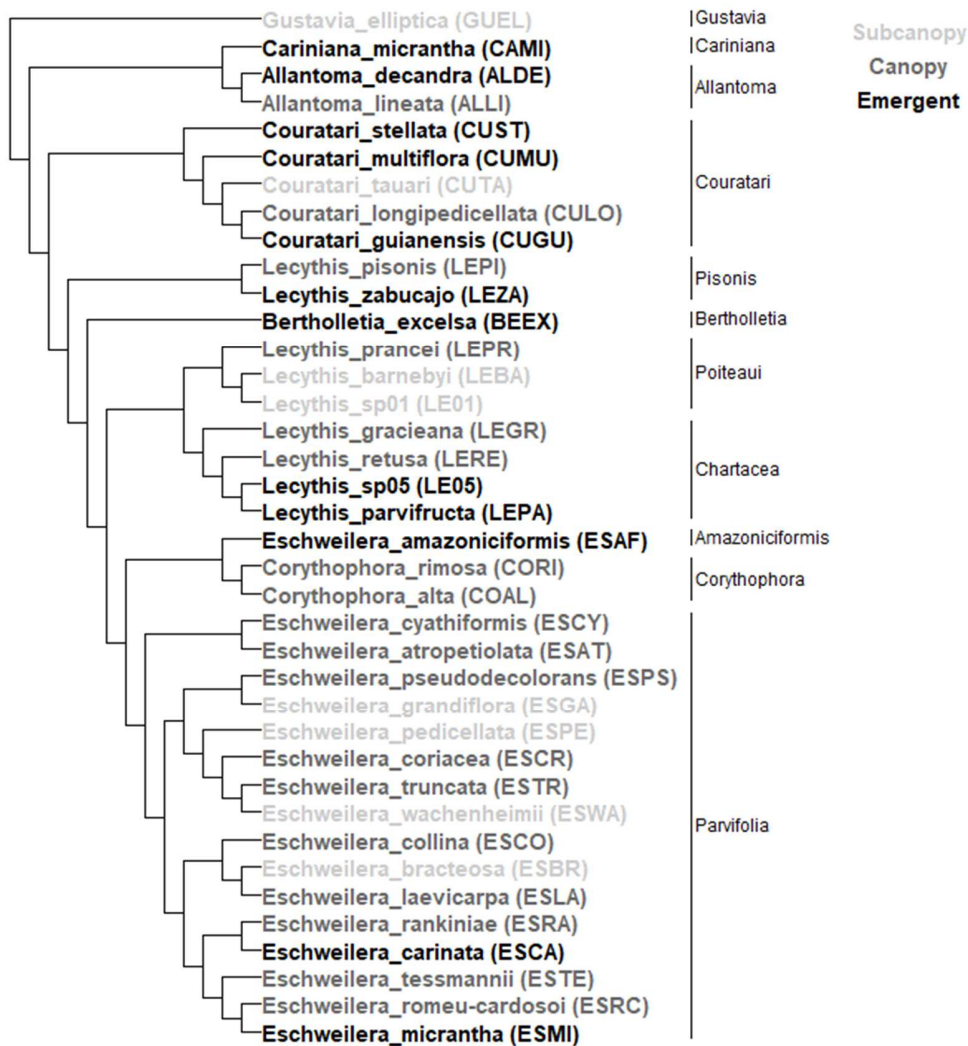
154   individuals sampled for molecular work) were changed. If a DNA collection was made from an

Fig. 2: Cladogram, with tips showing taxon names and species codes in parentheses. Clade shown on the right (Vargas et al., in prep). Height class shown by color of tip label.

155   individual in the plot, sequenced, and the subsequent phylogenetic analysis showed with high

156   confidence that that individual was in a clade other than its original identification, the

157   identification was changed. Two *Lecythis* species in the plot have not yet been formally

158   described because reproductive material has not yet been collected (Mori and Lepsch-Cunha,

159   1995). These undescribed species are designated *Lecythis sp.01* and *Lecythis sp.05* in a

160   Lecythidaceae monograph that outlines their vegetative characteristics (Mori and Lepsch-Cunha

161   1995; Mori et al. 2001).

162   Lecythidaceae are currently in the process of taxonomic re-circumscription based on

163   recent phylogenetic analyses, particularly *Lecythis* and *Eschweilera,* which are polyphyletic

164   lineages (Vargas et al. in prep). All *Eschweilera* species in the plot are in the Parvifolia clade

165   apart from *E. amazoniciformis*, which will form a monotypic genus in the revised taxonomy

166   (Vargas et al. in prep). The *Lecythis* species in the plot fall into three clades – Chartaceae (*L.*

167   *gracieana, L. parvifructa, L. retusa*, *L. sp05*), Pisonis (*L. Pisonis, L. zabucajo*), and Poiteaui (*L.*

168   *barnebyi, L. prancei, L. sp01*) (Fig. 2).

169   ***Demographic and biomass analyses:***

170   A randomization analysis was used to determine whether stem density (individuals ha^{-1}),

171   species richness (species ha^{-1}), basal area (m^2 ha^{-1}) and biomass (Mg ha^{-1}) differed between the

172   two censuses. Hectare values were resampled with replacement 1000 times, and the mean values

173   of each resample were calculated. The differences between means in 1989 and in 2019 were

174   calculated, and if ≤ 2.5% (two-tailed, α=0.05) of the mean differences overlapped 0 then the

175   years were considered to be significantly different. All individuals surviving from the first to the

176   second census were used in growth analyses apart from those that decreased by more than 25%

177   of their initial DBH, which we considered to be measurement error (30 individuals), and the few

178   broken trees for which only a resprout could be measured. Growth rate was calculated as $(DBH_{t2)}$

179   $– DBH_{t1})*10/(t_2-t_1)$ and is expressed in (mm yr^{-1}). Relative growth rate was calculated as

180   $(ln(DBH_{t2})–ln(DBH_{t1})/t$, expressed in cm cm^{-1} yr^{-1}. For species-specific demographic and

181   biomass analyses, individuals not identified to species (*Lecythis sp*., *Eschweilera "sagotiana"*)

182   were excluded, as were the two presumed hybrid individuals (*E. wachenheimii x coriacea*)

183   (Larson et al., 2021). Annual percent mortality was calculated as $m = (1- (N_s/N_0)^{1/t})*100$, where

184   N_s is the number of surviving stems, N_0 is the number of stems at the beginning of the census

185   interval, and t is the length of the census interval in years (Sheil et al., 1995). Annual percent

186   recruitment was calculated as $r = 1 - (N_s/N_t)^{1/t} -1)*100$ where Ns is the number of surviving

187   stems, N_t is the number of stems in the second census, and t is the length of the census interval in

188   years. This is the final-density-based annual recruitment equation, in which recruits are assumed

189   to suffer the same mortality as pre-existing individuals, which offers symmetric comparisons to

190   annual mortality (Kohyama et al., 2018).

191   A linear model with post-hoc Tukey HSD tests to determine among which height classes

192   (subcanopy, canopy, emergent) and habitats mean annual growth rates differed. Linear

193   regression models were used to determine whether species percent mortality and recruitment

194   differed as a function of mean species DBH$_{t1}$ and whether percent recruitment changed as a

195   function of abundance$_{t1}$. A Kruskal-Wallis test was used to determine whether there were

196   significant differences in annual percent mortality or recruitment among species height classes.

197   Individual probability of survival (1 = survival, 0 = mortality) as a function of size was analyzed

198   using a binomial generalized linear mixed effects model, with DBH$_{t1}$ and adult height class as

199   fixed effects and species as a random effect.

200   Aboveground biomass was estimated using the R package "BIOMASS" (Rejou-Mechain

201   et al., 2017), which includes inputs of species-specific wood density, where possible, as well as

202 latitude/longitude coordinates which account for variation in height-diameter relationships as a

203 function of environment where height is not available (Chave et al., 2014). For 27 of the species,

204 these data were available from the TRY database (Adler et al., 2014; Chave et al., 2009; Falster

205 et al., 2015; Kattge et al., 2020; Paine et al., 2015; Wright et al., 2007; Zanne et al., 2009). When

206 more than one value was available for a given species, values were averaged, and the mean value

207 was used to calculate biomass. For one species (*Couratari tauari*) where TRY values weren't

208 available but the "BIOMASS" package had species-level wood density values for the South

209 American Tropics, that value was utilized. When a species-level value was not available, the

210 generic average was used (13 species including all individuals not identified to species, hybrids,

211 and *Eschweilera bracteosa*, *E. rankiniae*, *E. romeu-cardosoi*, *E. cyathiformis*, *E.*

212 *pseudodecolorans*, *E. laevicarpa*, *Lecythis barnebyi*, *L. retusa*, *L. sp01*, and *L. sp05*). Analyses

213 were carried out in R version 3.6.3 (R CoreTeam, 2020).

214 ***Habitat definition and analyses:***

215   Subplots of size 10x10m were assigned to one of six habitat types; flood disturbed

216 habitat, ravine, slope, concave, convex, and plateau, as modified from Kenfack et al (2014) based

217 on *a priori* knowledge of the topography, soil characteristics, and past flooding in the plot.

218 Cutoffs of 60m and 99m, 15˚, and zero were used for elevation, slope, and convexity,

219 respectively. There is a distinctive plateau in the eastern part of the plot with geomorphological

220 characteristics separate from the rest of the plot (Mori and Becker, 1991), therefore is

221 categorized as its own habitat. There are also sandy ravines with small seasonal streams that

222 occur below 60m, the largest of which flows north to south in the middle of the eastern half of

223 the plot (Mori et al., 2001). Subplots were assigned to the flood disturbed habitat if more than

224 half of the subplot fell within areas mapped as flooded by Mori & Becker (2001). While the

225 flood disturbed areas are largely nested within the concave habitat, we chose to categorize them

226 as a distinct habitat to examine the way that these heavily disturbed areas differ in demographic

227 and biomass dynamics from other low-lying areas in the plot. Concave and convex habitats are

228 distinguished by whether water is likely to be retained in a subplot (concave), or runoff into a

229 nearby subplot (convex). Ravine subplots have an elevation of <60m; slope subplots have a

230 mean elevation ≥ 60 and < 99m and a slope of ≥ 15 degrees. Concave subplots have a mean

231 elevation of ≥ 60m and <99m, slope < 15 degrees, and convexity ≤ 0. Convex subplots have a

232 mean elevation of ≥ 60m and < 99m, slope < 15 degrees, and convexity > 0. Plateau subplots

233 have a mean elevation of ≥ 99m. Subplot slope and convexity were determined using the

234 fgeo_topography function in the "fgeo" package in R (Lepore et al., 2019).

235   Linear mixed effects models were used to analyze change in stem density, species

236 richness, and biomass over time among habitats. Density, richness, and biomass were modeled as

237 a function of fixed effect factors time and habitat, and a random effect of 10x10 subplot. A

238 bootstrapping analysis was used to detect differences in percent mortality and recruitment among

239 habitats. The number of 10x10 subplots that make up a given habitat were sampled randomly

240 with replacement from 10x10 subplots in that habitat, and annual percent mortality and

241 recruitment were calculated. This was done 10,000 times, and 95% confidence intervals for

242 mortality and recruitment were generated for each habitat. If these confidence intervals were not

243 overlapping, recruitment and mortality were determined to be significantly different in those

244 habitats.

245   A torus translation analysis (Harms et al., 2001) was used to identify species habitat

246 associations for both censuses. Random translated coordinates which maintained the spatial

247 relationships between individuals but shifted the x and y coordinates by a randomly generated

248   number between the minimum and maximum plot coordinates were generated 9999 times. When

249   an edge was reached, the coordinates wrapped around to the alternate side of the plot. For each

250   translation, the relative abundance of each species in each habitat was calculated. If the observed

251   relative abundance of a species in a habitat was greater than or less than the torus-translated

252   relative abundance in that habitat $\geq 97.5\%$ of the time ($\alpha=0.5$, two-tailed), there was determined

253   to be a significant positive or negative habitat association, respectively.

254   **Results:**
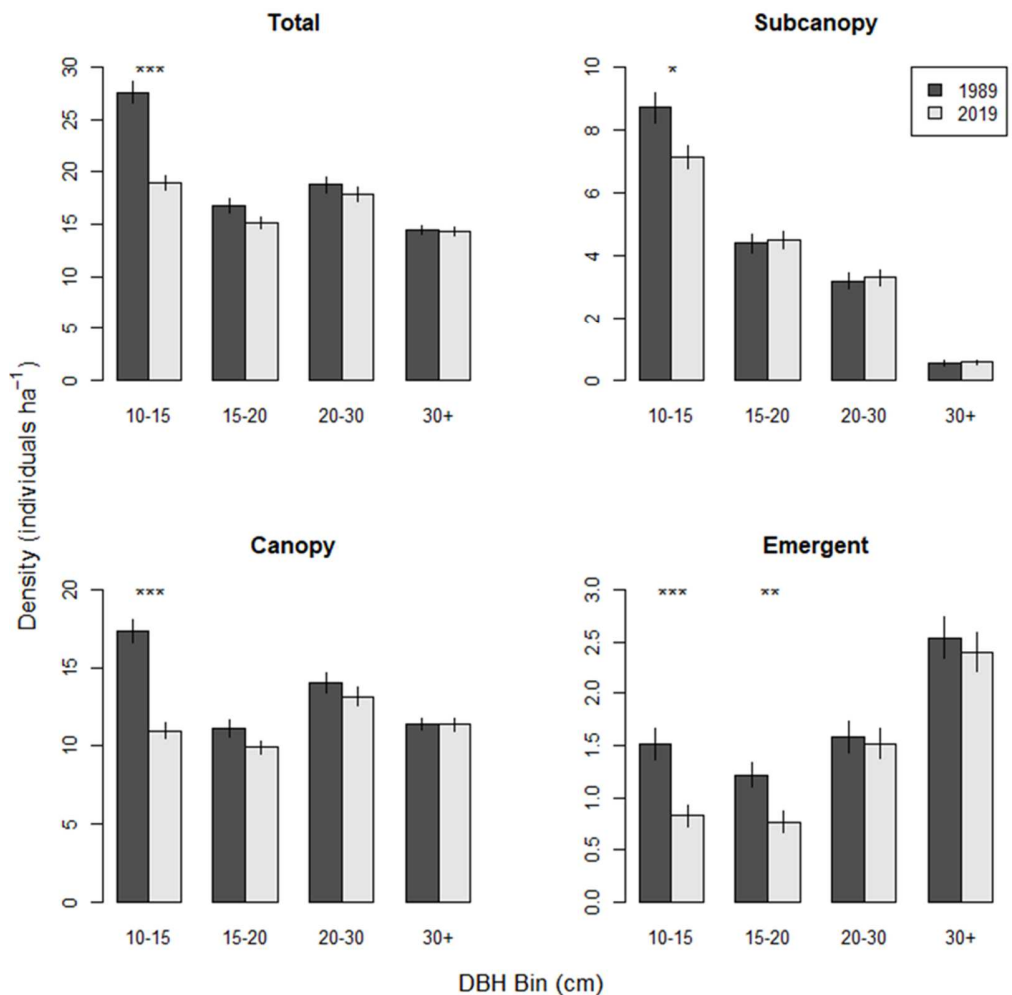
Fig. 3: Mean density of individuals ha^{-1} in DBH bins in 1989 (dark gray bars) and 2019 (light gray bars) for all individuals (top left), subcanopy species (top right), canopy species (bottom left), and emergent species (bottom right). Black bars represent standard error. Asterisks indicates a significant difference: p <0.0005 (***), p<0.005 (**), and p<0.05 (*).

255   We recovered 6741 Lecythidaceae trees in the 2019 census, representing 37 species

256   (Table S1). *Eschweilera coriacea* remained the most abundant species, with 1369 individuals,

257   followed by *E. truncata* with 1166 individuals, and *E. wachenheimii* with 894 individuals. As

258   few as 33 and as many as 134 individuals were found in a hectare, and the average density of

259   Lecythidaceae per hectare was 67.3±16.3 (mean ± SD). This is a significant decrease (p<0.0005)

260   from 1989, which had a mean density of 77.6±19.9 trees per ha. Species richness per hectare

261   ranged from 9 to 23, and the average species richness per hectare was 16.3±2.5, a significant (p <

262   .05) decline from 17.3±2.6 species in 1989. Two species (*Cariniana micrantha* and *Allantoma*

263   *lineata*) increased in abundance, *Lecythis sp.05* maintained its abundance, and the rest

264   experienced a net loss of individuals. Total plot basal area decreased slightly from 376.3 m^2 to

265   366 m^2. There was not a significant difference between mean basal area in 1989 (3.76±.086 m^2

266   ha^{-1}) and in 2019 (3.66±0.92 m^2 ha^{-1}).

267   The total number of individuals in all DBH classes (10-15cm, 15-20cm, 20-30cm,>30cm)

268   decreased between the two censuses (Fig. 3). The largest decrease was seen in the smallest DBH

269   class across all species. Among all subcanopy species, there was an increase in individuals in all

270   bins except 0-15cm. There were no increases among all canopy or emergent species in any DBH

271   bin (Fig. 3).

272   ***Demography***

273   Growth rates on average were low, with high intraspecific variation. Average growth

274   across all individuals (5681) during the 30 years between censuses was 36.9±32.6 mm

275   (mean±SD), or 1.2±1.1mm year $^{-1}$, and average relative growth rate was .0056 cm cm^{-1} yr^{-1}.

276   Average species annual growth rate ranged from 0.55±0.99 mm year $^{-1}$ (*Lecythis barnebyi*,

277   subcanopy) to 3.12±2.4 mm year $^{-1}$ (*Cariniana micrantha,* emergent), and annual relative growth
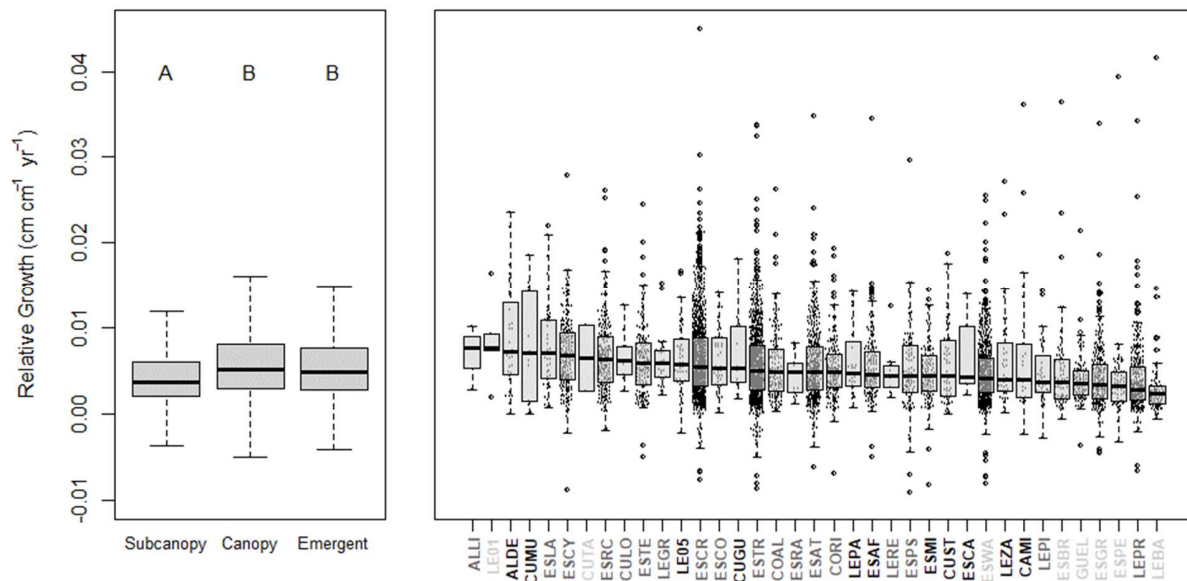
Fig. 4. Left: boxplot of annual relative growth (cm cm^{-1} year^{-1}) by height class, non-shared letters represent significant differences. Right: boxplots of annual relative growth per species, all individual data points shown behind boxplots. Species code color represents height class: light gray = subcanopy, medium gray = canopy, black = emergent.

278   ranged from 0.009±0.006 cm cm^{-1} yr^{-1} (*Allantoma decandra*, emergent) to 0.003±0.005 cm cm^{-1}

279   yr^{-1} (*L. barnebyi*) (Fig. 4). Five out of the six species with the lowest relative growth rates were

280   subcanopy species, and the subcanopy height class had significantly lower mean annual relative

281   growth than either canopy or emergent height classes. There was not a significant difference in

282   relative growth between canopy and emergent heigh classes, while emergents had higher mean

283   annual growth (cm yr^{-1}).

284   A total of 960 recruits (into the 10cm size class) were found during the 2019 census,

285   which is 0.51% annual recruitment. The riparian specialist *Allantoma lineata* had the highest

286   percent recruitment, with an initial abundance of 5 individuals and 3 recruits. Eight species had

287   zero recruits (that survived to the second census, *Eschweilera. micrantha, E. collina, E.*

288   *rankiniae, E. carinata, Lecythis. barnebyi, L. sp01, Couratari tauari, Bertholletia. excelsa*).

289   There was no relationship between species plot abundance in 1989 and percent recruitment

290   (p>0.1, R^2 = -0.02), and there are no significant differences in percent recruitment among height

291 classes (Fig. 5). Additionally, there is no relationship between annual percent recruitment and

292 mean DBH in 1989 (Fig. 5). There was no relationship between percent recruitment and percent

293 mortality among species (Fig. S1).

294   One quarter of the trees (1982 individuals, 25.54%) died in the thirty years between

295 censuses; an annual mortality rate of 0.98 percent. Mortality was more than double the
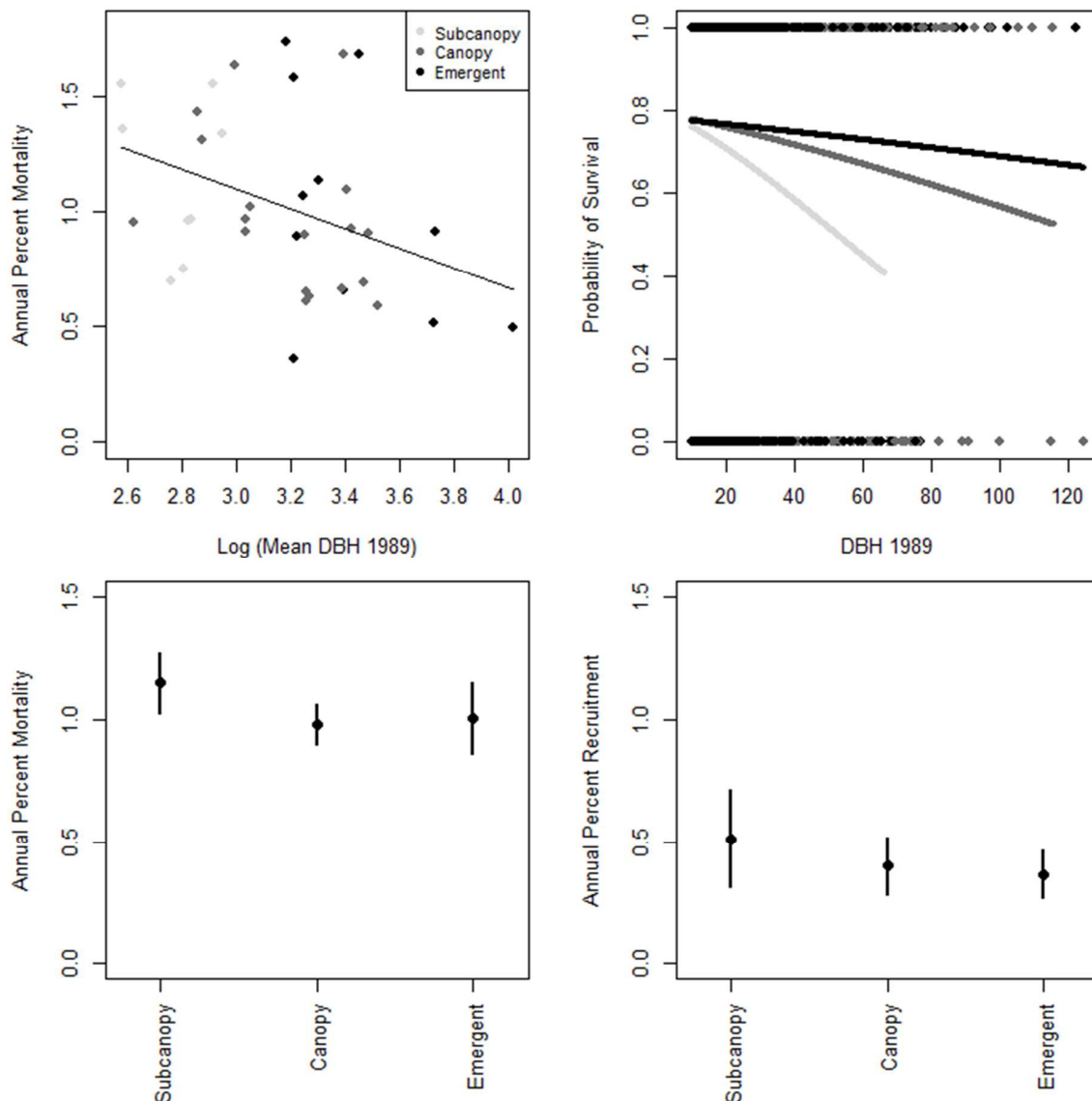
Fig 5. Top left: Species annual mortality as a function of mean DBH$_{t1}$. Regression indicates a significant relationship ($p<0.05$). Top right: Probability of survival as a function of DBH$_{t1}$ for each height class. Binary survival data for each individual (survived = 1, died = 0) shown as points. Bottom Mean and standard error percent mortality (left) and recruitment (right) by height class.

296 recruitment, resulting in a net loss of 1023 individuals ≥ 10cm DBH (13.2%). Percent mortality

297 decreased as a function of mean species DBH_{t1} (R^2 = .16, p < 0.05, linear regression), while

298 percent recruitment did not (Fig. 5).

299   A generalized linear mixed model was used to determine how the probability of survival

300 changes as a function of DBH, and whether that relationship differs among height classes. The

301 effect of DBH_{t1} on survival is more dramatic for subcanopy species than for canopy or emergent

302 species (Fig. 5). There was no significant effect of DBH on survival for emergent species, and

303 the relationship between size and survival differs significantly between subcanopy and both
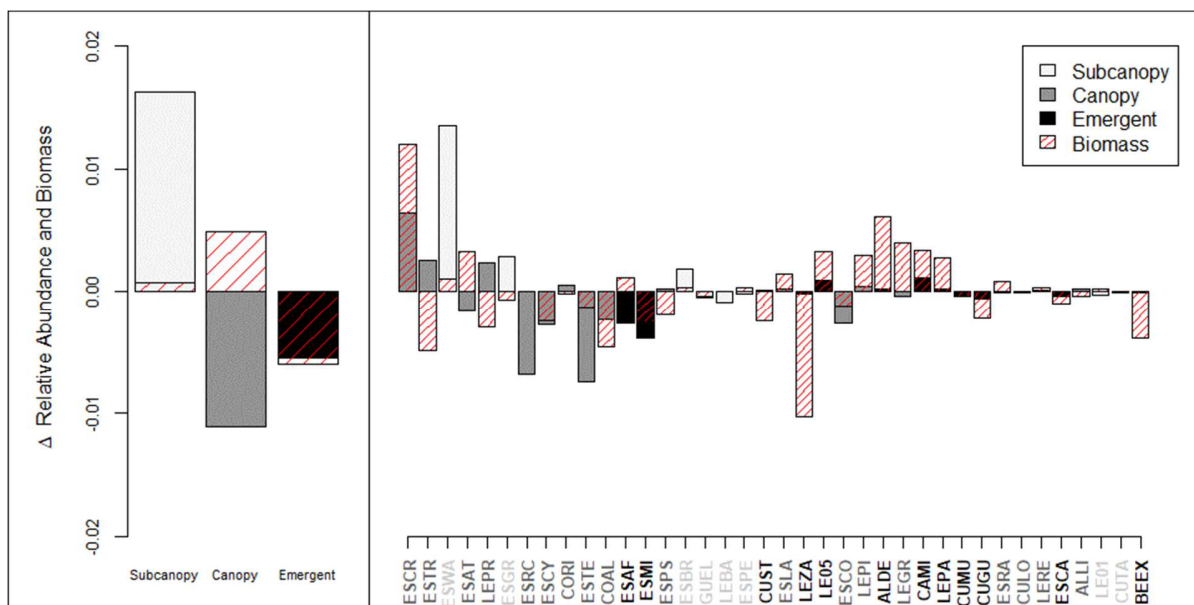
304 canopy and emergent species.

Fig. 6: Change in relative abundance (grayscale bars) and relative biomass (red hatched bars) by
height class (left), and species (right). Species ordered left to right by decreasing abundance.

305 **Biomass:**

306   Total aboveground living biomass (AGB) of Lecythidaceae during the first census (1989)

307 was 5143.33 Mg, and during the second census (2019), it was 5129.13 Mg. There was not a

308 significant decrease in mean biomass ha^{-1}, which was 51.4±14.2 Mg ha^{-1} in 1989 and 51.3±15.5

309 Mg ha^{-1} in 2019. Growth contributed an increase of 1430.87 Mg, mortality contributed a

310 decrease of 1544.95 Mg, and recruitment contributed an increase of 99.89 Mg. The aboveground

311 biomass of subcanopy species increased by 2.53 Mg (0.59% of initial subcanopy AGB), canopy

312 AGB increased by 14.61 Mg (0.39% of initial canopy AGB), and emergent AGB decreased by

313 33.45 Mg (3.45% of initial emergent AGB). Species with unknown height class contributed an

314 increase of 2.53 Mg of AGB. The highest changes in relative abundance were seen among

315 abundant species in the plot (Fig. 6). While there was a net loss of both subcanopy and canopy

316 individuals, subcanopy species increased in relative abundance, in large part due to an increase in

317 relative abundance of *E. wachenheimii*. Canopy and emergent height classes experienced a

318 decrease in relative abundance. Relative biomass change, however, was distributed across rare

319 and common species, and changed most in emergent species. The largest increase in biomass

320 was contributed by *E. coriacea*, a canopy species and the most common species in the plot,

321 followed by *Allantoma decandra*, a relatively rare emergent species. The species with the largest

322 decrease in relative biomass was *L. zabucajo* (emergent), largely due to loss of a few very large

323 individuals, followed by *E. truncata* (canopy), the second most abundant species in the plot.

324 *Lecythis zabucajo*, while having the largest decrease in relative biomass in the plot, saw only a

325 small decrease in relative abundance.

326   Emergent species tended to have a much more significant change in relative biomass than

327 relative abundance, while subcanopy species and most canopy species had the opposite.

328 Subcanopy species had an overall increase in relative abundance and very small increase in

329 relative biomass, while canopy and emergent species had a decrease in relative abundance.

330 Canopy species increased in relative biomass, and emergents were the only height class to

331 decrease in relative biomass. Emergent species account for only ~8% of individuals, but for ~

332 18% of AGB in the plot.
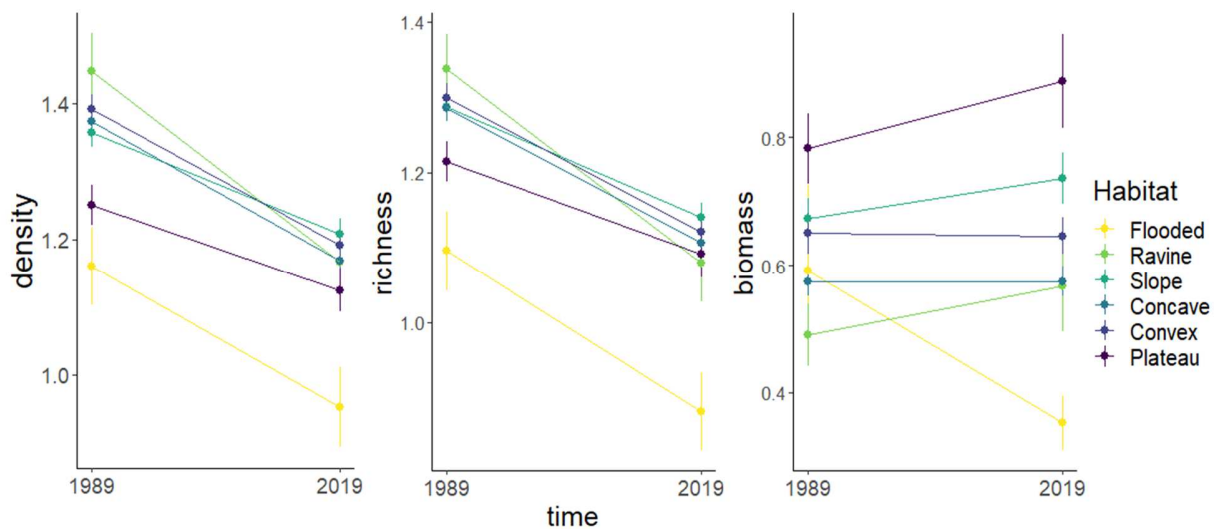
Fig. 7. Change in density (individuals), richness (species), and AGB (Mg) per 10x10m subplot between the two censuses across habitats.

333 *Habitat:*

334   The concave habitat was the most common (32.66 ha), followed by the slope (25.07 ha),

335 convex (24.81 ha), plateau (10.17 ha), and flood disturbed (3.07 ha) habitats. Density of

336 individuals and species richness per 10x10m subplot decreased significantly between 1989 and

337 2019 in all habitats. Density in the flood disturbed habitat was significantly lower than the

338 ravine, concave, and convex habitats in 1989, and significantly lower than all habitats in 2019.

339 Richness was significantly lower in the flood disturbed habitat than all other habitats except for

340 the plateau in1989, and significantly lower than all habitats except for the ravine in 2019. The

341 decrease between 1989 and 2019 in density and species richness was not different among

342 habitats. Biomass in 1989 was similar among all habitats. In 2019, the flood disturbed habitat

343 had significantly lower biomass than the slope, convex, and plateau habitats. The flood disturbed

344 habitat is the only one to have experienced a significant change in biomass – biomass decreased

345 significantly by 73.8 Mg AGB, or 60% of initial AGB.
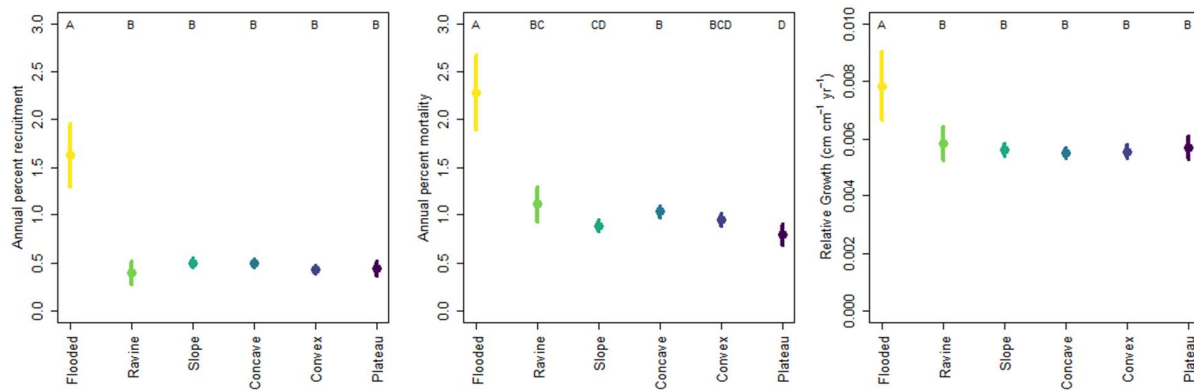
Fig. 8: Annual percent recruitment, mortality, and relative growth across habitats. Mean and 95% confidence intervals shown. Habitats that do not share a letter represent significant differences among groups.

346   In the whole plot, relative mortality of the three height classes was proportional to their

347   initial relative abundances, while in the flood disturbed habitat a disproportionately high number

348   of deaths were emergent individuals, and a disproportionately low number were subcanopy.

349   Mortality in the flood disturbed habitat was higher than in any other habitat. Additionally,

350   mortality in the ravine was significantly higher than on the plateau, and mortality in the concave

351   habitat was significantly higher than both slope and plateau habitats (Fig. 8). Bootstrapped

352   confidence intervals generated for annual percent recruitment of the flood disturbed habitat do

353   not overlap with any other habitat, showing that the flood disturbed habitat had significantly

354   higher recruitment than any other habitat (Fig. 8). The flood disturbed habitat also showed

355   significantly higher relative growth rates than all other habitats (Fig. 8).

356   All species with ≥ 100 individuals (n=18) were analyzed for habitat associations in 1989

357   and in 2019 (Table S2). There were a total of 22 significant habitat associations in 1989 (12

358   positive, 10 negative), and 19 significant habitat associations in 2019 (10 positive, 9 negative).

359   The plateau had the largest number of habitat associations both in 1989 (7) and in 2019 (6), and

360   the ravine had the smallest, with none in 1989, and one in 2019. There were 7 changes in habitat

361   association between the two time points, 3 of which occurred in the plateau: three species that

362   were positively associated with a habitat in 1989 demonstrated no association with that habitat in

363   2019, two negative associations became neutral, one neutral relationship changed to a negative

364   association, and one neutral relationship changed to a positive association. In five of the seven

365   changes, however, the species relative abundance was greater or less than the null relative

366   abundance 95% of the time (α=0.1, two-tailed) (Figs. S2 & S3). The two above this significance

367   level were *Eschweilera pseudodecolorans* losing a negative association with the concave habitat,

368   and *E. pedicellata* gaining a positive association with the plateau. *Eschweilera coriacea*, *E.*

369   *cyathiformis*, and *E. pseudodecolorans* had the highest numbers of significant associations in

370   1989 (3), and *E. coriacea* and *E. cyathiformis* remained the species with the highest number of

371   significant associations in 2019 (3). *Eschweilera coriacea* is the only species with two significant

372   positive associations, which were consistent across years. The convex habitat is the only to show

373   no differences in associations over time (Table S2).

374   **Discussion:**

375   This study reports on the demography, biomass changes, and habitat associations of

376   Lecythidaceae in mature Amazon rain forest. The intention with the initial establishment of the

377   Lecythidaceae plot, over 30 years ago, was to provide baseline data to be monitored over time

378   and compared to other plots (Mori et al., 2001). We determined how demographic and biomass

379   dynamics vary among species, height classes, and habitats in the plot, and how species are

380   partitioning environmental niche space.

381   *Demographic dynamics*

382   Growth rates in the Lecythidaceae plot are slow, averaging 1.2±1.1 (mean±SD) mm yr^{-1}.

383   In BDFFP, the average growth rates of trees above 10cm DBH in mature forests is 1.6 mm yr^{-1}

384   (Nascimento et al., 2005), which is slightly higher than the Lecythidaceae plot, but includes a

385   wider range of life history strategies including pioneer species. Long-term annual growth and

386   maximum (upper decile) growth is similar to Lecythidaceae species in other BDFFP inventory

387   plots (Chambers et al., 1998; Laurance et al., 2004). Growth is slower than the global wet

388   tropical forest average of 4.7 mm yr^{-1} (Locosselli et al., 2020), as this Central Amazon forest has

389   high wood density and slow turnover relative to forests with higher nutrient soils (Muller-

390   Landau, 2004). There was large variation in relative growth among individuals of a given

391   species. This is expected as growth is highly dependent on site conditions of light, moisture,

392   herbivory, and soil (Chambers et al., 1998; Nascimento et al., 2005; Rüger et al., 2011). Growth

393   differs significantly among height class with subcanopy species showing slower relative growth

394   rates than canopy and emergent species. Canopy and emergent species did not differ in relative

395   growth, but emergent species had higher absolute growth.

396   Total recruitment in the plot lagged mortality, causing a net decrease in individuals.

397   Although there is evidence of increasing demographic turnover in the Amazon over the past

398   several decades (Phillips et al., 2008), a lower relative increase in recruitment than mortality has

399   caused a net decrease in number of stems since 1983 (Brienen et al., 2015), consistent with our

400   trend. Plot recruitment was lower than Lecythidaceae recruitment in five hectares of undisturbed

401   upland forest in the same area over five years between 1981 and 1986 (Rankin-de-Merona et al.,

402   1990). The same study also found higher recruitment than mortality among Lecythidaceae, while

403   we found the opposite to be true. The area in that study was much smaller, and therefore more

404   sensitive to environmental and demographic stochasticity. Alternatively, it may be possible that

405   Lecythidaceae are, on average, recruiting less successfully than they were 35 years ago, although

406   additional monitoring is required to confirm this. There is no difference in recruitment among

407   height classes, nor does percent recruitment change as a function of mean species DBH,

408   therefore a stature-recruitment trade-off is not detected among Lecythidaceae species, likely

409   because the smaller-statured species are still relatively long-lived – no species exhibit a short-

410   lived breeder functional type (Rüger et al., 2020).

411   Mortality was high relative to recruitment in our study; there was a net loss of >1000

412   individuals, in contrast to recent findings of increasing prevalence of the genera *Eschweilera*,

413   *Corythophora*, and *Couratari* (Esquivel-Muelbert et al., 2019; Laurance et al., 2004). The

414   increase in other studies was attributed to taller statured and fast-growing species in these genera,

415   however many of the *Eschweilera* in our study are slow-growing subcanopy and canopy species

416   and therefore not likely to drive this increase. At the species level, mortality decreased as a

417   function of mean DBH, thus tends to be lower in larger-statured species (Fig. 5). At the

418   individual level, the decreased probability of survival with increasing DBH is characteristic of

419   tropical forests, where the highest risk of mortality occurs at the seedling stage (Uriarte et al.

420   2004; Iida, Poorter, et al. 2014; Ma et al. 2014) and is often U-shaped, with an uptick in

421   mortality risk at large sizes. The smallest individuals in the plot are 10 cm DBH, thus it would be

422   expected that survival probability decreases with DBH having already made it to the adult stage

423   (King et al. 2006; Rüger, Huth, et al. 2011; Iida, Kohyama, et al. 2014). Large trees may be more

424   prone pathogenic damage, experience increased water limitation, be at increased risk of

425   structural instability and windthrows, and experience higher reproductive costs (Coomes and

426   Allen, 2007; Iida et al., 2014; Mencuccini et al., 2005). Size has been shown not to have a strong

427   effect on probability of survival in larger-statured, non-pioneer species (Uriarte et al., 2004), and

428   mortality has been shown to be low at larger DBH for emergent species (Clark and Clark, 1992),

429   in line with the negligible decrease in probability of survival with increasing DBH for emergent

430   species that we found.

431   *Habitat and demography:*

432   A particularly impactful La Niña year occurred in 1989 after the plot was established, in

433   which standing water of up to 1m was seen in six areas in the plot (Mori and Becker 1991).

434   Relative growth rates in the flood disturbed habitat were significantly higher than in any other

435   habitat. The flooded habitat also showed the highest rates of recruitment and mortality,

436   signifying increased dynamism in these disturbed areas. Relative to sandier valleys, t*erra firme*

437   plateaus tend to have higher soil clay content, and therefore increased nutrient levels (Laurance

438   et al., 2006), which may account for the higher mean DBH and annual growth on plateaus than

439   the lower-lying habitats, although relative growth rates were similar among all non-flood-

440   disturbed habitats. Alternatively, there may be more large-statured species on the plateau,

441   however only two emergent species were abundant enough to include in the habitat association

442   analysis. While the low concave habitat is likely more similar to the flood disturbed habitat in

443   soil properties, it experienced less disturbance and therefore did not have the same increased

444   light availability leading to high relative growth rates.

445   In addition to the flood disturbed habitat, the other habitats associated with increased

446   moisture or standing water, the ravine and the concave habitats, saw higher mortality than the

447   plateau, and the concave habitat had higher mortality than the slope (Fig. 8). While plateaus tend

448   to be at increased risk of seasonal moisture limitation, lower-lying streams and swampy areas

449   have been shown to increase mortality risk of seedlings (Johnson et al., 2017), and the same risks

450   of hypoxic conditions and soil erosion may similarly increase adult mortality. Additionally, there

451   may be an increased number of drought-resistant species on the plateau, mitigating moisture

452   limitation risk. In this plot, among Lecythidaceae individuals, too much moisture seems to be a

453   larger risk to survival than not enough.

454   High plot mortality cannot be explained entirely by the flooding event, however it did

455   increase overall mortality in these areas and differential relative mortality among size classes.

456   Rainfall data suggest 2008-2009, another intense La Niña year, may have been comparable to

457   1989 (Marengo et al., 2012). Water accumulation in low-lying *terra firme* is known to occur

458   elsewhere (Pearson and Derr 1986; Myster 2007), however, the effects on long-term

459   demographic and biomass dynamics are not well understood. El Niño and associated droughts

460   are often discussed as a significant source of disturbance in Amazonia (Laurance et al., 2004;

461   Wright, 2005), and while La Niña is also known to increase mortality in Amazonian forests

462   (Aleixo et al., 2019), La Niña-associated flooding warrants future study given its potential to

463   influence demography and biomass dynamics of Amazon forests.

464   ***Biomass dynamics***:

465   Although there was a decrease in individuals in the plot, AGB remained relatively stable

466   – growth and recruitment nearly balanced AGB loss from mortality. Lecythidaceae can be

467   estimated to account for about 5.5% of species richness, 10.5% of individuals (De Oliveira and

468   Mori, 1999), and about 15% of AGB in a hectare at BDFFP (Baker et al., 2004b). Thus, the

469   contribution of Lecythidaceae to the density of individuals in the forest is disproportionately high

470   given its species richness, and its biomass contribution is disproportionately high given its

471   density.

472   Species that have changed the most in relative abundance are different from those that

473   have changed the most in relative biomass, the latter which tend to be emergent species. Biomass

474   change is due largely to mortality and growth of large trees. Although many small trees died and

475   recruited into the plot, these contributed relatively little overall to biomass dynamics over the

476   past 30 years. Biomass is highly correlated with stem density in the plot, with the most abundant

477 species contributing the most biomass. An exception is the large contribution of the one *B.*

478 *excelsa* to plot biomass in 1989, and the outsize contribution of some emergent species such as *L.*

479 *zabucajo*. Emergent species accounted for only 12.4% of the decrease in individuals, but for the

480 entire net decrease in ABG. There are no emergent species in the top 10 most common

481 Lecythidaceae species in the plot, and no emergent species have abundances above 200

482 individuals, but they account for nearly 20% of ABG in the plot. This outsize contribution to

483 biomass dynamics points to the importance of accounting for height class and life history when

484 considering conservation tactics, selective logging, and a forest's capacity to sequester carbon.

485   While the biomass decrease seen in the plot was small, it is contrary to a current trend of

486 positive net biomass change in trees ≥10 cm DBH in the Amazon over the past several decades

487 (Baker et al., 2004a). This trend varies, however, including at other BDFFP plots (Baker et al.,

488 2004a), and the biomass increase has decelerated in the recent past (Brienen et al., 2015). Natural

489 disturbance regimes can lead to a decrease in AGB, including increased mortality in waterlogged

490 areas (Baker et al., 2004a; Ferry et al., 2010). The net decrease in AGB in flood-disturbed areas

491 is larger than the total net loss of AGB in the plot, and only flooded quadrats have significantly

492 decreased in biomass.

493   Sources of disturbance additional to flooding have been documented in the surrounding

494 areas during the time between censuses. These include blowdown events that caused high

495 mortality and biomass loss (Negrón-Juárez et al., 2010; Nelson, 2005; Nelson et al., 1994), as

496 well as two El Niño drought years. Given the large time interval (30 years) without intermediate

497 biomass observations, the magnitude of other disturbances is unknown, however they may have

498 contributed to the higher-than-average mortality and lack of increase in biomass across the

499 censuses. Additionally, if disturbance resulted in differential mortality of smaller trees, or

500 subsequent decline in long-lived understory trees as blowdowns might be expected to, a decrease

501 in recruitment may be seen due to mortality of recruits before they enter the 10-cm size class

502 (Nelson, 2005). Given the slow growth of Lecythidaceae, it is likely that the time since

503 disturbance has not been long enough to cause the subsequent increase in biomass seen

504 elsewhere.

505   Individuals above 10cm contribute over 95% of AGB, therefore the biomass dynamics

506 that we observed based on individuals greater than 10cm should largely parallel overall

507 Lecythidaceae biomass dynamics in the plot (Chave et al., 2003). Because Lecythidaceae is a

508 dominant family in many parts of the Amazon, the decrease in biomass in this study, even if

509 slight, underlies the importance of continued monitoring.

510 *Habitat Associations*

511   A torus translation analysis illuminated 22 significant habitat associations in the first

512 census, and 19 in the second. There is no significant relationship between species abundance and

513 number of significant habitat associations, thus being common in the plot is not a function of

514 habitat generalization or specialization. Five of the 6 generalist species (no significant positive or

515 negative habitat associations) in 1989, and 4 of the 6 in 2019, were subcanopy species. This

516 suggests that species in the subcanopy height class may be less likely to specialize than taller

517 statured species, however we are limited in this analysis by the rarity of many species in the plot;

518 only two emergent species were abundant enough to include in the habitat association analysis.

519 The plateau located on the eastern part of the plot is the most dynamic habitat – it experienced

520 the highest number of changes in habitat associations. Habitat associations in the flood disturbed

521 habitat are similarly stable as other habitats (only one difference between the two censuses). This

522 similarity suggests associations in 2019 were not a function of shifting species composition due

523   to a single disturbance between censuses, thus flooding in these areas may be less anomalous

524   than previously assumed. No associations changed from positive to negative, or vice versa – the

525   changes were between neutral associations and a significant association, and 5 of the 7 neutral

526   associations associated with those shifts were nearly significant, thus we conclude that habitat

527   associations are generally stable in the plot.

528   *Eschweilera coriacea*, the most abundant species in the plot, is significantly positively

529   associated with the flood disturbed and the concave habitat and has a significant negative

530   association with the plateau. This demonstrates a preference for high moisture *terra firme*

531   habitats and an ability to tolerate flooding. It is known to occur in seasonally inundated *várzea*

532   habitat (Mori et al., 2010) therefore adaptations to low-oxygen conditions may contribute to its

533   ability to dominate in occasionally flooded *terra firme* forest. *Eschweilera pseudodecolorans* and

534   *L. prancei* were found to be plateau species in a forest divided into two habitat types – valley and

535   plateau/slope (Cosme et al., 2017; Oliveira et al., 2019), consistent with our finding them

536   positively associated with the plateau. *Eschweilera coriacea* has been defined as a generalist (not

537   restricted to either the valley or the plateau) (Oliveira et al., 2019), however its P_{50} (the water

538   potential at which 50% loss of conductivity occurs) is similar to the mean P_{50} value among valley

539   individuals. Additionally, *E. coriacea*, analyzed as part of a species complex in the Parvifolia

540   clade, was found to dominate over other species in areas with increased topographic wetness

541   (Schmitt et al., 2021). While currently one of the most locally and regionally dominant lineages,

542   increasing drought risk associated with climate change may alter the composition of

543   competitively dominant species.

544   The second most abundant species in the plot, *E. truncata*, previously defined as a

545   plateau/slope species (Oliveira et al., 2019), is positively associated with the convex habitat,

546   which has a higher mean elevation, higher runoff and likely less soil moisture than the flood

547   disturbed or concave habitats. The two most abundant species in the plot, therefore, show non-

548   overlapping positive habitat associations. Additionally, none of the sister species pairs in the plot

549   share habitat associations, and none of the seven most abundant species in the plot share positive

550   habitat associations. This is in line with other studies demonstrating habitat specialization as a

551   niche partitioning mechanism (de Oliveira et al., 2014), and likely contributes to the coexistence

552   of many closely related species in the plot.

553   *Conclusions*

554   Lecythidaceae is a clade of slow growing, mature forest trees that have significant

555   economic and ecological value. Accurate demographic information for species, some which are

556   exploited for timber, is integral to sustainable logging operations. In a *terra firme* forest in the

557   Brazilian Amazon, a post-logging growth increment of 4-5 mm yr^{-1} with 1% mortality was

558   deemed necessary to sustain a 40 year reduced-impact logging cycle (Sist and Ferreira, 2007). Of

559   the three species in our study that are commonly logged (*Cariniana micrantha*, *Eschweilera*

560   *coriacea* and *Couratari guianensis*) only *C. micrantha* has a 90th percentile growth rate (a proxy

561   for light gap growth) > 5 mm yr^{-1}, and none have a mean growth rate of > 4 mm yr^{-1}.

562   *Eschweilera coriacea*, has a 90th percentile growth rate < 3 mm yr^{-1}. While dynamics and

563   therefore requirements for sustainability and regeneration may differ by forest, the slow growth

564   rates in our study suggests a 30-year logging cycle is not sustainable, even under high light

565   conditions. Our height class- and habitat-specific demographic information, particularly

566   mortality, may also be of use to improve the parameterization of simulation models used for

567   forest management (van Gardingen et al., 2006).

568   The Amazon, like many places in the world, is experiencing more extreme weather

569   events as a function of climate change. This may alter forest abiotic conditions such as moisture

570   availability; understanding species-habitat associations can allow us to consider how habitat

571   changes might influence forest composition and biomass dynamics. As intended with its

572   establishment, this plot continues to provide integral baseline data for a large area of mature,

573   undisturbed forest, that can be used to compare dynamics to the nearby fragmented forest, and to

574   other Amazon forests that are being impacted by human land use and climate change.

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