1 **Modeled changes on functional diversity and carbon storage driven by drought in the**

2 **Amazon forest: a plant-trait vs. PFT-based comparison**

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21 **Abstract**

22 The drought impacts on functional diversity and how it modulates the Amazon carbon sink

23 remain poorly understood, although evidences point that changes in functional richness,

24 divergence and evenness can possibly change carbon stocks while keeping unchanged other

25 ecosystem properties like vegetation structure. Here we investigate how a 50% reduction in

26 rainfall can affect functional diversity and thereafter carbon stocks in the Amazon. We used

27 two modelling approaches in which functional diversity is or is not predefined: one model

28 version uses a plant functional type approach (PFTA; fixed trait values in 3 tropical PFTs) and

29 the other uses a varying trait-based approach (TBA; semi-random combination of trait values

30 creating 3000 plant life strategies). Six functional traits were considered as fixed/variant:

31 carbon allocation and residence time on leaves, aboveground woody tissues and fine roots.

32   The imposed drought caused a widespread and similar magnitude loss of carbon storage in

33   both approaches (~60%). Nevertheless, the geographical patterns of loss differed, with TBA

34   showing more subtle changes along the basin, mainly on its southern limits. Also, the TBA

35   presented an increase in fine roots investment (~10%), whereas the PFTA reduced carbon in

36   all plant compartments. Changes in functional diversity were different in magnitude and

37   direction between approaches: TBA(PFTA) showed changes, for fine roots allocation, of

38   +19.33%(+4.94%) in richness; +276.54%(-74.71%) in evenness and -26.01%(+0.15%) in

39   divergence, resulting in a functional reorganization of plant community allowing previously

40   rare trait values to increase its density and a change in functional composition. Our results

41   demonstrate that the inclusion of higher functional diversity did not show a significant

42   difference in total carbon loss, mainly because the carbon assimilation processes

43   (photosynthesis and respiration) did not differ between model versions. Notwithstanding, the

44   different modeling approaches regarding carbon allocation and residence time suggest that

45   varying-trait vegetation modeling offers a promising, though still underexplored, method to

46   represent and better understand changing functional diversity and plant-trait distribution in

47   light of biogeochemical processes that standard DGVMs do not allow.

48   **Keywords:** trait-based modeling, climate change, carbon allocation, functional composition,

49   functional richness, functional evenness, tropical forest

50   **Introduction**

51   The possible modification in Amazon forest's ability to absorb and store carbon due to

52   climate change is permeated with uncertainties (Finegan et al., 2015), and the role of

53   functional diversity (the values, ranges of values and relative abundance of functional traits in

54   a given community or ecological unit; Díaz et al, 2007) on this ecosystem process is poorly

55 explored (Poorter et al., 2015; Sakschewski et al., 2016; Sitch et al., 2008). Dynamic Global

56 Vegetation models (DGVMs) have been widely used to explore the question from a

57 biogeochemical perspective (Cramer et al., 2001; Scheiter, Langan, & Higgins, 2013)

58 providing substantial contribution to our current knowledge of the Amazon forest ecology and

59 resilience (Díaz & Cabido, 1997; Prentice et al., 2007; Scheiter, Langan, & Higgins, 2013).

60 For instance, the projected possibility of a large-scale degradation of the Amazon forest

61 driven by severe climatic changes (Cox, Betts, Jones, Spall, & Totterdell, 2000) and the role

62 of soil phosphorus as a limiting factor to CO_2 fertilization in the region (Fleischer et al.,

63 2019), are all results derived out of studies using DGVMs.

64 Nonetheless, the results of DGVMs regarding the future of Amazon forest's carbon stock are

65 contradictory and diverge both on the magnitude and on the direction of change (Huntingford

66 et al., 2013; Powell et al., 2013; Rammig et al., 2010). The different climatic scenarios,

67 parameterization and model formulation (e.g. nutrient limitations to CO_2 fertilization) may be

68 some possible reasons for such a degree of uncertainty (Huntingford et al., 2013; Quillet,

69 Peng, & Garneau, 2010; Sitch et al., 2008; Verheijen et al., 2015).

70 Additionally, the poor functional trait diversity represented in DGVMs in the tropics is

71 another feature that can potentially lead to inaccurate estimates of the impacts of

72 environmental changes on ecosystems, especially in hyperdiverse (at least in the taxonomic

73 sense) ecosystems such as the Amazon forest (Aguirre-Gutiérrez et al., 2019) . This is because

74 it is reasonable to expect alterations on the environmental filtering following climatic

75 changes, and hence, the requirements for an individual to be successful may change as well

76 (Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010). It implies that the physiological

77 tolerances determined by functional traits are also modified, possibly generating a

78 rearrangement of the community traits distribution (e.g. frequency and occurrence) and

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79 selection for alternative functional structure, composition and diversity of forest community,

80 modifications already observed in other studies (Enquist et al., 2015; Thompson, Mackey,

81 McNulty, & Mosseler, 2009; Wieczynski et al., 2019). Functional diversity can be

82 decomposed in three components: richness, divergence and evenness, that can respond

83 differently to disturbances and that play different roles on plant communities. The

84 rearrangement above cited together with modifications on functional diversity components

85 can in turn affect the forest suitability and resilience to the new climatic conditions as has

86 been shown in some observational studies (Aguirre-Gutiérrez et al., 2019; Enquist & Enquist,

87 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019).

88 The ability of the majority of DGVMs to capture such plant community rearrangement is very

89 limited (Fyllas et al., 2014; Scheiter, Langan, & Higgins, 2013) since they commonly use the

90 concept of plant functional types (PFTs) to represent vegetation (Reu et al., 2014; Scheiter et

91 al., 2013; Verheijen et al., 2015). It means that the vegetation is represented in a very small,

92 discrete, and *a priori* defined set of plant types. In that sense, the diversity of responses and

93 the possibility for selecting alternative strategies that deal better with the new climate

94 condition present very limited boundaries (Fyllas et al., 2014; Mori, Furukawa, & Sasaki,

95 2013). It possibly hampers advancements in the comprehension of the yet unknown effects of

96 climate change in functional diversity and other ecosystem processes driven by or emerging

97 from plant diversity (Díaz & Cabido, 2001; Lavorel & Garnier, 2002).

98 In order to overcome these limitations that a PFT approach imposes, some vegetation models

99 - the so-called trait-based vegetation models - claim to represent plant trait diversity in a less

100 discrete manner (Fyllas et al., 2014; (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013);

101 Sakschewski et al., 2016; Scheiter et al., 2013). This type of vegetation model replaces the

102 fixed parameters that represent functional traits in PFTs by variable ones (Pavlick, Drewry,

103   Bohn, Reu, & Kleidon, 2013; Reu et al., 2014; Webb, Hoeting, Ames, Pyne, & LeRoy Poff,

104   2010; Wullschleger et al., 2014), allowing a more functionally diverse representation of the

105   responses of vegetation to a given environmental condition (Scheiter et al., 2013). It timely

106   provides the opportunity for models to look beyond biogeochemical variables creating

107   potential for exploring a multiplicity of functional ecology-related questions (Sakschewski et

108   al., 2016; Darela-Filho et al., in prep.), many of them still unexplored, such as the role of the

109   different components of functional diversity on resilience against environmental changes.

110   Notwithstanding, the ability of trait-based models to effectively improve the representation of

111   biogeochemical cycling and the representation of ecological processes that are commonly

112   considered in standard DGVMs is yet to be assessed, as well as the comparative difference in

113   the response of vegetation, in terms of functional diversity, to environmental changes when

114   the trait-based approach is or is not considered.

115   In this article we employed a vegetation model applied for the Amazon region in a scenario of

116   persisting drought. Two modeling approaches were used - one with low functional diversity

117   (PFT approach) and one with high functional diversity (trait-based approach) - to investigate

118   three main questions: (i) how do the modeling approaches differ in their results regarding the

119   Amazon forest capacity to absorb and store carbon under the drought scenario?; (ii) what is

120   the drought impact on the different components of functional diversity for both modeling

121   approaches?; and, finally, (iii) what is the role of the functional diversity level and the

122   impacts of drought on it to the response of the two modeling approaches regarding the carbon

123   storage?

124   **Materials and methods**

125   *The CAETÊ model: an overview*

126 As a trait-based model, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ)

127 model focus on representing a higher variability of plant functional traits and, whenever

128 possible, the range of functional diversity found in plant communities. As such, vegetation is

129 represented by a set of functional strategies (called as plant life strategies, PLS), being that

130 each of which is a unique combination of functional traits values. The combination of such

131 trait values describes the ecophysiological behavior of plants and their relationship with the

132 environment. These traits control, for example, the differential acquisition of carbon, light and

133 water, ultimately defining how the strategy copes with the environment and, together with the

134 other PLSs of the community, determine ecosystem functioning (Figure 1).

135 The underlying premise to create these PLSs is that the range of values of a functional trait

136 observed in nature can be regarded as one axis of a multidimensional hypervolume formed by

137 the combination of n chosen functional traits (Blonder, 2017; Villéger, Mason, & Mouillot,

138 2008). In that sense, each point inside of this hypervolume is a unique combination of values

139 for each of the functional traits, a PLS. The volume that all points together occupy can be seen

140 as a functional trait space. The values of functional traits that compose the hypervolume are

141 semi-randomly sampled from the complete range of values (to more details see Appendix

142 A.1). The combination of all sampled values generates a large number ($>10^5$) of combinations

143 within the functional space. As for other trait-based models (e.g. Pavlick, Drewry, Bohn, Reu,

144 & Kleidon, 2013; Reu et al., 2011), CAETÊ follows the assumption that sampling an

145 appropriate number of PLSs from the potential functional space (see sensitivity test in

146 Appendix A.2) combined with an environmental filtering mechanism together with a

147 representation of competition allow the model to produce reasonable biogeochemical and

148 functional diversity patterns.

149   The environmental filtering mechanism acts in the model such that each PLS within the trait

150   space performs differently under the same environmental conditions (e.g. temperature and

151   precipitation; Diaz, Cabido, & Casanoves, 1998; Webb et al., 2010). All grid cells are

152   initiated with the same set of PLSs (number and identity) in a condition analogous to a bare

153   soil. Therefore, even tough all trait combinations are equally probable to occupy a given grid

154   cell and each of them has its particular climatic occurring space, it is expected that some PLSs

155   will survive and present different performances and abundances (percentage occupation of the

156   grid cell weighted by their biomass; Appendix A.3.1) and some of them will perish in the first

157   simulation steps. PLSs that do not survive are excluded from the grid cell (and cannot be

158   reestablished in that grid cell in this model version).

159   The differential survival and abundance between PLSs are made possible because each

160   functional trait in the model is related to at least one trade-off (cost-benefit relationship)

161   leading to different relative performances and ability to deal with the environment. The trade-

162   offs also prevent the model from creating the so-called "Darwinian demons" (i.e. maximizing

163   all the functions that contribute for fitness; Scheiter et al., 2013). Since functional traits both

164   respond to and affect ecosystem-level processes (Díaz et al., 2013; Funk et al., 2017; Lavorel

165   & Garnier, 2002) the varying PLSs ecophysiological performance generates heterogeneous

166   biogeochemical fluxes and stocks and functional diversity through space and time. Such

167   model outputs are aggregated to the grid cell scale according to the modeled abundances of

168   PLSs, which are determined on the basis of the biomass-ratio hypothesis (Grime, 1998). A

169   table with each functional trait and its respective trade-off and equation can be found in Table

170   A.3. An in-depth description of the CAETÊ model can be found in Appendix A.3.

171   *Simulation setup*

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172 In this study we employed, for the Amazon basin, a non-dynamic version of the CAETÊ

173 model, which calculates equilibrium solutions based on long-term mean monthly climate

174 variables (for the period between 1980 and 2010). A spinup simulation period of ????? years

175 was carried out to initialize carbon stocks in different plant compartments (see Appendix

176 A.3.4).

177 Two sets of model runs were carried out: one employing, as the majority of current vegetation

178 models, a PFT approach (with a low functional diversity initialization: 3 PFTs) and the other

179 using a trait-based approach (with a high functional diversity initialization: 3000 PLSs).

180 Despite the difference in the number of plant types and in the way that functional traits values

181 are chosen, the general model formulations and principles are the same for both model

182 approaches.

183 Since our focus of analysis here is on the process of carbon storage, we set the functional

184 traits related to the percentage of the carbon distributed to plant compartments (carbon

185 allocation) and the carbon residence time in each plant compartiment (how long the carbon

186 stay in each compartment) to be variable between PLSs/PFTs. Plants are split into three

187 compartments: leaves, aboveground woody tissues (hereafter ABGW) that represents stem

188 and branches, and fine roots; hence, six functional traits are considered as variable: the

189 allocation and the carbon residence time for each of the plant compartments. Together, these

190 functional traits ultimately define the amount of carbon in each compartment of a PLS or PFT

191 at each time step, and are of primary importance for determining absorption and storage of

192 carbon in the whole study area (Chambers, Fisher, Hall, Norby, & Wofsy, 2012; Fatichi &

193 Leuzinger, 2013; Malhi, 2012; Norby et al., 2005).

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194 Three tropical PFTs were defined in the PFTA to describe the vegetation and the parameters

195 that represent the functional traits used for this study are *a priori* defined following previous

196 literature (Table A.1). The use of only tropical PFTs is justified given the study area (Amazon

197 forest), and with them, we tried to encompass the majority of PFTs previously used in

198 standard DGVMs for this region. In the trait-based model approach, the initial range of values

199 for each functional trait (from where some of them will be sampled to create the

200 hypervolume) are indicated in Table A.2. The ecophysiological processes linked to each

201 functional trait, its trade-offs, and associated formulations are summarized in Table A.3 and

202 described in Appendix A.3.2. It is important to highlight that CAETÊ admits the use of any

203 functional trait of interest, as well as any number of them, as long as the trait is linked to

204 existing model formulation and can have trade-offs implemented. CAETÊ works in a spatial

205 resolution of 0.5º x 0.5º and is coded mainly in Fortran 90 with some modules written in

206 Python.

207 *Input data*

208 The following climatic data were used as inputs for the model: air surface temperature,

209 precipitation, shortwave radiation, relative humidity and atmospheric CO_2 concentration. The

210 first three variables were obtained from mean monthly data for the period between 1980 to

211 2010. These data are available in the Inter-Sectoral Impact Model Intercomparison Project 2

212 (ISI-MIP2; Warszawski et al., 2014). Atmospheric CO_2 concentration was obtained from the

213 National   Oceanic   and   Atmospheric   Administration   platform

214 (http://co2now.org/images/stories/data/co2-mlo-monthly-noaa-esrl.pdf), using the mean value

215 of [CO_2] for the same period of the climatic data (1980-2010).

216 *Representation of functional diversity and composition*

217 Here we focused in a large-scale analysis of functional diversity for the whole Amazon basin,

218 in opposition to a detailed grid cell-by-grid cell analysis. In that sense, the value of each of the

219 six variant functional traits in each grid cell is represented by a mean value that is estimated

220 according to the relative abundances of PFT/PLSs (see Appendix A.3.1) using the

221 Community Weighted Mean (CWM) metric (Díaz et al., 2007; Grime, 1998).

222 Additionally, functional diversity is regarded here both from the perspective of its single-trait

223 components as well as its multi-trait component (i.e. the combination of traits). The single-

224 trait element allows to interpret more precisely how the different traits interact (affects and

225 responds) with the environment (Lepš, de Bello, Lavorel, & Berman, 2006; Ricotta &

226 Moretti, 2011), while the multi-trait component gives information about the ecological

227 strategy as a whole (i.e. as a syndrome), incorporates the relations between the traits,

228 including its trade-offs, and also how the community occupies the given possible functional

229 space (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016; Blonder, Lamanna,

230 Violle, & Enquist, 2014).

231 We considered that single-trait functional diversity can be decomposed in three components

232 following Carmona et al. (2016) definitions and methods: (i) functional richness: the portion

233 of the total functional trait space[1] that is occupied in an ecological unit derived from the

234 variance of trait values of all the considered organisms (PFT/PLSs in our case); (ii) functional

235 evenness: how regular is the density distribution of the PLSs' or PFTs' trait values in the

236 functional trait space; (iii) functional divergence: the degree to which the abundance of

237 PFT/PLSs' trait values are distributed towards the extremes of their functional trait space.

238 Carmona's method uses probability density distributions for the calculation of the

239 components, the so-called TPD's (trait probability distribution).

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1 [1] Here, functional trait space is the total range of values for a specific functional trait.

For multi-trait functional diversity we used the hypervolume metric following Blonder et al. (2014). Hypervolumes can combine the distribution of n trait values and then calculate functional diversity components (Barros et al., 2016; Blonder et al., 2018), for example, the volume size, that indicates how much of the possible functional space an ecological unit occupies (i.e. the variance of values; Barros et al., 2016), that can be interpreted as functional richness. Also, the distribution of values within the hypervolume informs, together with the centroid (that indicates the mean values), about system functional composition.

As recommended by Barros et al. (2016) we performed a principal component analysis (PCA) with a centered and scaled method (see Figure SM.1.). PCA was also necessary because our traits are correlated (e.g. the allocation for one is correlated to the allocation in the others) and, it was also necessary in order to reduce , since the number of variables (six) exceeds the suggested number of variables for constructing the hypervolume in the used metric (Blonder et al., 2014). Then, the PCA allows the delineation of the hypervolume using the factor scores of the chosen PC's. Additionally, the PCA indicates the trade-offs that emerge from the model results. All the analyses were performed in the R platform. We used the package *TPD* (Carmona, 2019) for the analysis of single-trait functional diversity, the package *hypervolume* (Blonder, 2019) for the analysis of multi-trait functional diversity, and the function *prcomp* of the package *stats v3.6.2* (R core team, 2013) for the PCA.

The role of functional diversity on ecosystem response to environmental change

To test the potential effects of functional diversity on the ecosystem's biogeochemical response to drought, we applied a homogeneous reduction of 50% on precipitation for the whole Amazon basin. In this model application we were interested in understanding if a plant community with higher functional diversity (trait-based approach) responds differently to a

263   drier climate in its ability to store and partition carbon compared to a community with lower

264   functional diversity (PFT approach). For this we compared the degree of change in carbon

265   stock either considering the whole plant or the compartments separately. To complement this

266   analysis, we looked into the underlying mechanisms that generate the difference of response

267   by exploring the effects of drought on functional diversity and composition *per se* (see next

268   section).

269   *Functional composition and diversity response to drought*

270   For the single-trait framework analysis, we compared the TPDs generated by the two climatic

271   conditions for all the six traits: regular climate and reduced precipitation. For this, the

272   dissimilarities between the two TPDs were computed by calculating the degree of overlap

273   between the two distributions (dissimilarity index that can vary from 0 – completely

274   functionally similar - to 1 – completely functionally different; Carmona, de Bello, Mason, &

275   Lepš, 2016). This index shows if functional structure of the community was significantly

276   modified by the climate scenario (Carmona, de Bello, Mason, & Lepš, 2019). We also

277   compared how the three facets of functional diversity aforementioned changed after the

278   applied disturbance.

279   For the multi-trait framework four hypervolume were constructed and compared: one with

280   regular climate and other with reduced precipitation for each of the modeling approaches.

281   After performing the PCA (a previous necessary step explained in section *Representation of*

282   *functional diversity and composition*) the hypervolumes were delineated using the factor

283   scores of the three first principal components (PCs) since they were able to explain more than

284   98% of the variance. It is important to highlight that we needed to calculate the PCA with

285   both climatic conditions and for the two modeling approaches together (Barros et al., 2016),

286 after that, separate hypervolumes were calculated from the factor scores corresponding to

287 each climatic condition and model approach dataset. After constructing the four

288 hypervolumes we were able to compare them in terms of size (richness), the distance between

289 the centroids (to verify the change inon mean values) and the degree of overlap through

290 Jaccard similarity index that range from 0 (completely dissimilar) to 1 (completely similar).

291 These three metrics together can give us an idea of the magnitude of change in functional

292 diversity and composition with drier climate considering plant ecological strategies as a

293 whole.

Results

Drought impacts on carbon storage and partitioning

296 The reduction in precipitation caused a considerable basin-wide reduction of carbon stocks

297 both for the high and low degrees of functional diversity employed in the model: -57.48% and

298 -57.45%, respectively. Also, for both approaches this reduction was higher in regions with

299 naturally lower precipitation levels, mainly in southern, central and northern parts of the basin

300 (Figure 2a and 2b). However, the spatial pattern of carbon loss driven by the imposed drought

301 condition differs between the trait-based (hereafter TBA) and PFT approaches (hereafter

302 PFTA). The TBA was able to maintain carbon in some areas where the PFTA has lost it

303 completely. This is more evident in naturally drier areas, such as the transition between the

304 Amazon forest and the savannah (*cerrado*) and central Amazon. It is noteworthy also that the

305 loss of carbon in TBA is more gradual, i.e., there is a smoother gradient between a grid cell

306 value and its neighboring cells, and also across different basin regions. On the other hand, in

307 the PFTA the carbon loss is more abrupt both between neighboring cells and across the

308 regions of the basin.

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309 Despite the similar magnitude in the total carbon storage change, specific plant compartments

310 have shown different patterns of changes when comparing the two approaches (Figure 2c and

311 2d for fine roots and Figure SM.2 for leaves and ABGW). None of the compartments has

312 shown, for any area, an increase in carbon stock with drought, except for the fine roots

313 compartment in TBA, indicating a change in carbon partitioning for the latter approach. This

314 increase, around 10% (blue areas in Figure 2d), was observed in the transitions from humid

315 and evergreen forest to the Brazilian savannahs (*cerrado*) and also in the basin northwest.

316 Even in areas where the root compartment has lost carbon in the TBA, it was in a lower

317 degree when compared to the other compartments and to the PFTA approach.

318 *Functional composition under a drier climate*

319 The applied drought scenario caused a modification on the density distribution of the six

320 variant functional traits both for PFTA and for TBA (Figure 3). For all the traits, the shape of

321 the curve changed considerably, reflecting on the dissimilarity index: all of them presented a

322 dissimilarity approximating to 1, which means that they became functionally different with

323 the new climatic condition (Table 1). For example for all of them, the maximum values of the

324 probability density distributions were lower under low precipitation, i.e., the peak of the

325 curves decreased, meaning that there was a clear and strong reduction in dominance for the

326 communities under drought. Because of the observed decrease in dominance other trait values

327 that were previously rare (i.e. very low density), or absent, were able to occur in the trait

328 space or increased their density, changing the shape of the curves, which ultimately

329 demonstrates a change in the functional composition of the communities and on the different

330 components of functional diversity.

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Nevertheless, the change in functional composition was different when comparing the modeling approaches. First, considering all the traits, the PFTA showed a trimodal distribution, with three clear and discrete peaks along the trait space when the precipitation is reduced, while in TBA the distribution showed a higher diversity of values that had their density increased, resulting in a much more diffuse distribution within the functional space. This pattern can also be seen when considering all traits together through the hypervolumes: for the PFTA it is possible to observe three clear data grouping under drought (Figure 4a), and a much less discretized data distribution from the TBA (Figure 4b). Also, for the TBA it is important to observe that the increase in the trait values density is more prominent for the ones that were previously rare under the regular climate conditions (Figure 3a-c and g-i). In that sense, the TBA showed a clear pattern with reduction in precipitation for traits related to allocation: an increase in density toward higher values of carbon in fine roots and an increase in density toward lower values of carbon in leaves and especially in ABGW. On the other hand, the PFTA showed a much smaller change, and changes in density values were restricted to a small area of the functional space, with almost no change in the range of values (Figure 3d-f and j-l). A similar pattern of density distribution change was found for the residence time traits: the PFTA showed an increase in residence time for leaves and fine roots (despite the very slight change) and a conservation in residence time values for ABGW, while for TBA we observed an increase in residence time for leaves and fine roots but a decrease for ABGW.

Functional diversity under drought scenario

The above-cited changes drove alterations in the three facets of functional diversity within the two employed modeling approaches (Figure 5). In general, we found an increase in functional richness for all traits in both approaches, but the percentage of change in this facet was much higher in TBA. Functional evenness showed an increase superior to 100% in TBA,

355 nonetheless, in the PFTA traits showed a decrease in this functional diversity component and

356 in a lower degree of change (74% maximum). As a whole, the TBA traits presented reduction

357 in divergence, while the opposite result was observed for the PFTA, also with the same

358 pattern found for the other functional diversity facets regarding the magnitude of change.

359 Also, with the applied drought scenario, the hypervolumes for TBA and PFTA showed a

360 pronounce change. (Figure 4; see movie SM.1 for a 3D animated representation). Under

361 natural climatic conditions the size of the volume that the data occupy was equal to 1.711 and

362 0.007 for TBA and PFTA, respectively; while under reduced precipitation the volume size

363 increased for both approaches: 47.837 for the former and 0.755 for the latter. It indicates an

364 increase in the occupation fraction of the functional space under a drier climate (i.e. increase

365 in the amplitude of trait's variation and richness) in a magnitude of 2,695.0% for the TBA and

366 1,025.0% for the PFTA. The overlap degree between hypervolumes (before and after the

367 drought scenario) yielded a value of 0.038 for the TBA and of 0.009 for the PFTA, indicating

368 almost no similarity of the hypervolumes. Finally, the distance between the centroids of the

369 two hypervolumes after imposed climatic change indicates the change on the mean values:

370 the centroid distance in the TBA was 5.25 and 0.937 in the PFTA (i.e. the mean values were

371 modified in a higher magnitude for the former approach).

372 **Discussion**

373 Briefly, our results showed:

374 • PFTA and TBA presented a similar magnitude decrease in total carbon storage

375 capacity with drought;

- The changes along the basin was much more smoother for TBA than PFTA with the former presenting carbon stock conservation in grid-cells where tha latter was not able to;

- All the plant compartments showed a reduction in storing carbon, except for an fine roots in TBA that presented an increase of investment in this tissue;

- Both modelling approaches presented changes on the three facets of functional diversity, however the magnitude of the change was much higher in TBA;

- Functional diversity modifications derived from a functional reorganization of communities, but because of the smaller diversity of possible combinations (3 PFTs), this reorganization PFTA was less conspicuous.

Ecological mechanisms

As expected, the 50% reduction in precipitation caused a pervasive decrease (~60%) in the basin carbon stock for both modeling approaches, concentrated mainly in naturally drier regions. This massive decrease of Amazon forest ability to store carbon in drought scenarios is in agreement with experimental (da Costa et al., 2010; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007), observational (Brienen, Phillips, Feldpausch, & et al., 2015; Enquist & Enquist, 2011; Phillips et al., 2009, 2010) and previous modeling studies (Lapola, Oyama, & Nobre, 2009; Powell et al., 2013; Rammig et al., 2010). In our model, this decrease is a result of the strengthened soil moisture stress that reduces photosynthetic rates and net primary productivity, meaning that the carbon available to be invested in plant compartments is reduced.

However, we expected a more pronounced difference between the TBA and PFTA since it is widely accepted that a more diverse (both taxonomically and functionally speaking)

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399   ecosystem tends to be more resilient to environmental changes (Cadotte, Carscadden, &

400   Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019).

401   However, the similar loss magnitude can be partly explained by the fact that the carbon

402   assimilation processes (photosynthesis and respiration) were not modified between the two

403   modelling approaches and some important processes (e.g. embolism) and functional traits

404   linked to drought response are still not included in the model (in the *Discussion* section some

405   caveats are presented).

406   Nevertheless, despite the similar magnitude in total carbon loss, the two approaches presented

407   differences on the geographical pattern of loss: the model approach with high initial

408   functional diversity (TBA) was able to maintain carbon in regions where the other approach

409   with low initial functional diversity (PFTA) lost it completely, especially in the southern and

410   central parts of the Amazon forest, even though the former lost carbon in a higher degree than

411   the second where both modeling approaches maintained carbon. This result at first may seem

412   contradictory, but can be explained by the fact that the mechanisms that underlie ecosystem

413   carbon loss was different between the approaches: while the PFTA showed, on average,

414   almost no change in the carbon partitioning with drought, the TBA increased the investment

415   in fine roots to the detriment of the investment in leaves and ABGW. It is well known that

416   climatic changes, such as drought, induce changes on C partitioning patterns (Doughty et al.,

417   2014; Kannenberg et al., 2019) including a prioritization of root investment at the expense of

418   other tissues (Doughty et al., 2014; Phillips et al., 2016; Rowland et al., 2014). In our model, a

419   higher investment in fine roots increases the uptake of water, which makes the community

420   better able to deal with drought and maintain carbon stocks or reduce the degree of loss. We

421   observed it in the TBA: an avoided of total carbon loss in grid cells where the PFTA was not

422   able to hold it. This happened because the TBA could make a carbon investment

423   rearrangement while the PFTA could not (the discussion of the reason is presented in the next

424   section).

425   The shift in carbon partitioning due to climate is of primary relevance for the future of

426   Amazon carbon stocks (Doughty et al., 2015; Friedlingstein et al., 2006) and is especially

427   important if the carbon is allocated towards pools with shorter turnover, such as fine roots or

428   even root exudates (Jiang et al., 2020), that contribute in a lesser extent to total carbon

429   biomass comparatively with other pools such as wood tissues (Chave et al., 2009; De Kauwe

430   et al., 2014; Kannenberg et al., 2019; Luo, 2003). Our modeling exercise captured well this

431   process: the drought lead to an increase in investment of fine roots in the TBA that provided

432   greater resistance to drought, preventing the total loss of carbon in several grid-cells, and also

433   caused a lower carbon storage in other tissues, mainly on ABGW and led to a relative lower

434   carbon storage in some locations when compared to the PFTA. In that sense, if the ability to

435   store carbon is used as the only proxy for ecosystem resilience, as is commonly used, (e.g.

436   Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016), it may result in

437   inaccurate interpretations about the response of tropical forests to climate change.

438   Lastly, since model formulation was equal in the two approaches, one can conclude that the

439   differences observed regarding carbon storage are derived from the initial functional diversity

440   employed and from the changes that the imposed climatic scenario caused on different

441   components of functional diversity.

442   *Forest functional reorganization*

443   Our results show that the applied long-term drought scenario caused a significant functional

444   community reorganization of Amazon forest in terms of composition, dominance relationship,

445   functional richness, evenness and divergence both for the PFTA and TBA. The functional

446   reorganization is supported by the dissimilarity values found between traits distributions

447   before and after the disturbance both in the single-trait and multi-trait analysis.

448   These results are in agreement with theoretical, experimental and modeling evidences that

449   show environmental change is able to cause a modification on functional structure (Enquist &

450   Enquist, 2011; Hillebrand, Bennett, & Cadotte, 2008; Mouillot, Villéger, Scherer-Lorenzen,

451   & Mason, 2011), dominance (Hillebrand et al., 2008; Schmitt et al., 2019; Valencia et al.,

452   2015), composition (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Nepstad,

453   Tohver, Ray, Moutinho, & Cardinot, 2007) and diversity components (Hillebrand et al., 2008;

454   Zhang, Chen, & Reich, 2012). In our simulations these changes occurred because the

455   environmental filtering was modified and, as a consequence, the selection of the strategies

456   changed towards favoring trait values that were previously rare or absent. Those changes

457   modified the abundance of traits and the way that communities occupy the functional space

458   (Carmona, de Bello, Mason, & Lepš, 2016, 2019; De Bello, Carmona, Mason, Sebastià, &

459   Lepš, 2013; Enquist & Enquist, 2011). Next sections explore the changes related to functional

460   dominance, composition and diversity components.

461   *Changing functional dominance*

462   The differential occupation of the functional space with drought was specially caused by the

463   change in dominance: an expressive decrease in abundance of a narrow range of trait values to

464   a wider one for all the considered traits, especially for the TBA. Dominance reflects the

465   distribution of traits in a community and plays a fundamental role on ecosystem processes,

466   such as carbon cycling (Cavanaugh et al., 2014; Ruiz-Jaen & Potvin, 2011), since,

467   theoretically, the dominant traits contribute more to aggregate processes in communities and

468   ecosystems when compared to rare ones (Hillebrand et al., 2008).

469   The dominance change modeled in our study and observed/theorized in the other studies cited

470   above, is in agreement with the theory that the shift in community dominance with a change

471   in climate could be caused by a compensatory dynamic process, also called as 'functional

472   density compensation': when the composition of an ecosystem adjust to the new conditions

473   enabling types of plants (or trait combinations, in our case) that previously exerted a less

474   relevant functional role (i.e. low density) to increase their dominance and vice-versa

475   (Gonzalez & Loreau, 2009; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016). As a

476   consequence, the diversity of traits values available in a community is central, since it can act

477   as an "insurance" for new environmental conditions (Fauset et al., 2015; Lohbeck, Bongers,

478   Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999). It also reinforces the importance

479   of rare trait values, functional strategies or species, for the maintenance of ecosystem

480   processes in future environmental conditions, including tropical forests that commonly

481   present a hyperdominance of species with specific functional traits (Cornwell, Schwilk, &

482   Ackerly, 2006; Jain et al., 2014; Mouillot et al., 2013; van der Sande et al., 2017).

483   Such a functional density compensation phenomenon was well captured in our modeling

484   results: reduced precipitation led to a consequent emergence of new strategies and/or increase

485   in abundance of previously rare trait values occurrence. However, the capacity of a

486   community to promote a compensatory dynamics strongly depends on its functional diversity

487   (Mori et al., 2013). This was clearly demonstrated in our work when comparing the PFTA and

488   the TBA. The functional space occupation as a consequence of the decrease in dominance was

489   different for the approaches, for example, the PFTA presented for all traits, a restricted

490   possibility of the occurrence of new trait values, presenting trimodal curves with drought. On

491   the other hand the trait-based approach showed a more spread occupation of the functional

492   space. This was also observed in the multi-trait analysis of functional diversity: the wider

493   occupation of the functional space with the reduced precipitation was much stronger in the

494   TBA when compared to the PFTA, as well as the centroid distance.

495   These contrasting results are due to the modeling approach-dependent difference in the

496   response diversity[2] that was imposed by the level of functional diversity in which the model

497   was initialized. Such a response diversity was very limited for the PFTA since it was provided

498   with only 3 possibilities of trait combinations, preventing better suited traits combination to

499   establish themselves under the new climatic conditions whereas the TBA was provided with

500   3000 possible trait combinations. It also explains why the carbon partitioning rearrangement

501   was so limited for the PFTA.

502   Also, the different diversity of responses within the approaches can explain the geographical

503   contrasts in the carbon loss. The smoother loss of carbon observed in the TBA was possible

504   because of its higher capacity of functional reorganization due to response diversity, selecting

505   better suited trait combinations in accordance with the grid-cell environment. Meanwhile, the

506   PFTA presents a reorganization very restricted because of its low diversity of responses and

507   the change of environmental conditions between one grid cell and another could not be

508   suitable for the 3 available trait combinations.

509   *Changing functional composition*

510   In the present study the different employed modeling approaches presented distinct responses

511   in terms of changes in community composition, which are mainly associated to the magnitude

512   of the change: while the change in the occupation of the functional space for the TBA showed

513   a prominent shift in allocation towards fine roots, in the PFTA the composition change is

514   much less remarkable, with the maintenance of the more abundant traits around the same

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2   [2] Diversity of responses that traits or trait combinations show to disturbances in a given
3   community (Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016)

515 range of values prior to the imposed climatic change. That means the TBA was able to select

516 strategies that coped better with the drought scenario by increasing fine roots allocation and

517 residence time, since this tissue is strictly related to the water uptake; likewise, the increase

518 observed in residence time for leaves in this employed approach, despite the decrease in

519 allocation, can be identified as a mechanism to maintain the levels of photosynthesis since the

520 reduction of allocation for this organ reduces total photosynthetic rates for a given plant

521 strategy.

522 In fact, literature shows that carbon partitioning can exhibit plasticity depending on water

523 availability (Bazzaz, 1991; Franklin et al., 2012; Weiher et al., 1999; Weiner, 2004).

524 According to the optimal partitioning theory, the preferential allocation should be directed

525 towards the organ responsible for the acquisition of the most limited resource, in that sense,

526 one should expect, as observed in the TBA results, an increase towards roots investment under

527 water limitation (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972). However,

528 the fate of carbon under drought conditions is still a matter of debate, and conflicting results

529 are found in literature (Hofhansl, Schnecker, Singer, & Wanek, 2015; Litton, Raich, & Ryan,

530 2007) but some pattern can be identified: apparently a mild drought, or stronger dry seasons,

531 lead to a higher investment in fine roots (Blessing, Werner, Siegwolf, & Buchmann, 2015;

532 Brando et al., 2008; Doughty et al., 2014; Lacointe, 2000; Rowland et al., 2014), while a more

533 persistent and severe drought could decrease allocation belowground followed by a higher

534 investment in wood and canopy tissues (Blessing et al., 2015; Sevanto & Dickman, 2015).

535 The investment in wood tissues could be explained by the fact that these organs maximize

536 plant hydraulic safety (Hofhansl et al., 2015).

537 In that sense, it seems that the impact of drought on allocation is not straightforward and may

538 depend on a series of variants that goes beyond carbon partitioning such as the duration,

539 severity of drought and other plants features like the sensitive to embolism and cavitation, not

540 yet addressed in the employed model formulation.

541 Comparing our results about the change in functional composition with other studies can be

542 tricky, once the result of studies regarding changes in functional composition is highly

543 dependent on the chosen traits. For example, Esquivel-Muelbert et al., (2018) and Aguirre-

544 Gutiérrez also found an increase in abundance of plants of the trait values of which confers

545 them a higher tolerance to drought. Despite of this obstacle in comparing the results, it is

546 undeniable that our employed TBA is able to at least identify this type of community level

547 change, and a promising next step is to include hydraulic, leaf and wood traits that has been

548 shown to be crucial to understand the response of ecosystems to drought (Barros et al., 2019;

549 Christoffersen et al., 2016; O. L. Phillips et al., 2010; Poorter et al., 2010). Our findings

550 related to functional traits composition become fundamental by allowing advances on the still

551 undergoing question of how functional shifts moderate drought-induced biomass loss and

552 forest resilience against environmental change.

553 *Functional diversity facets responses*

554 Few studies have explored how drought impacts the(Carmona, de Bello, Mason, & Lepš,

555 2016) different functional diversity components, despite the known importance of them for

556 ecosystem functioning and resilience (Carmona et al., 2016). Here we explored, for the first

557 time, the impact of drought on Amazon functional diversity considering its three primary

558 components: richness, evenness and divergence, and also examined functional diversity

559 considering all the six chosen functional traits together.

560 The observed impacts on functional diversity, for both modeling approaches, were a

561 reverberation of the community functional reorganization, especially the dominance change.

562 For functional richness we observed an increase in this variable for the two modeling

563 approaches but the magnitude of change was much higher for the TBA, what is highly

564 connected to the fact that the latter presents a wider range of possible values to occupy the

565 space, while this range is very limited for the former. It also reflected on the volume occupied

566 in the functional space considering the traits altogether: volume increases in both the

567 approaches, but the TBA showed an increase more than two fold stronger when compared to

568 the PFTA. This is contrary to the hypothesis that a harsher environment would decrease

569 functional richness by selecting a narrow range of strategies due to the environmental filtering

570 (Cornwell et al., 2006; Funk et al., 2017; Kleidon, Adams, Pavlick, & Reu, 2009; Perronne &

571 Gaba, 2017). However, the observed functional reorganization is able to explain this

572 unexpected result, since they allowed new combinations of traits to establish or increase their

573 occurrence (Mouillot et al., 2013). It means that, in some cases, functional richness can

574 increase in disturbance scenarios if the environmental change affects mainly the dominant

575 strategies or trait values.

576 Regarding evenness: the increasing evenness in the six functional traits observed for the TBA

577 means that the drought scenario made the distribution of trait values in the trait space to

578 become more regular. On the other hand, the PFTA showed a decrease in this functional

579 diversity component for the majority of traits. The evenness increase in TBA is tightly related

580 to the observed decrease of dominance and increase of abundance of trait values that were

581 very rare before the disturbance. The decrease in evenness for PFT approach can be explained

582 by the fact that the reduced precipitation decreased the dominance of a very restricted range of

583 trait values (dominance of one PFT) and allowed the occurrence of the other 2 PFTs. Since

584 the difference between the PFTs is very discretized, the occurrence of trait values ended up

585 concentrated in three peaks of density hence turning the distribution less even. Evenness can

586 also be interpreted as an evidence of the effectiveness in using the functional niche space: the

587 higher the evenness, the higher the utilization of the total functional space (De La Riva et al.,

588 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011).

589 Therefore, our results indicate that a change in the environment can force the community to

590 better occupy the functional niche space, if it presents a sufficient variability in its trait values,

591 as we observed for the TBA.

592 Lastly, the TBA presented a general decrease in divergence while the PFTA approach showed

593 an increase for this functional diversity facet. The decrease in divergence found for TBA

594 means that, regarding a specific trait, the values distribution is no longer concentrated in only

595 one extremity of the functional space, but other trait values that were not that important before

596 became significant for the community and for the ecosystem functioning with the

597 environmental change. Beyond that, divergence is also a way to understand if the frequency

598 distribution of trait values in the functional niche space maximizes the total community

599 variation in functional characters (Mason et al., 2005). In that sense, low divergence could be

600 a result of different, or even contrasting, strategies being able to deal with the new conditions

601 (Funk et al., 2017). The increase in divergence found in the PFTA is a product of the

602 emergence of the three peaks on traits distribution. For this approach a better occupation of

603 functional space (low divergence) is impossible considering its very low diversity of trait

604 values available.

605 *Conclusions*

606 In this study we aimed at understanding the role of functional diversity on the ability of

607 Amazon forest to store carbon under a persistent drought scenario (50% homogeneous

608 precipitation reduction). We employed the vegetation model CAETÊ with two levels of initial

609   functional diversity (low and high, PFT and trait-based respectively). In order to understand

610   the mechanisms that underlies the observed responses of each approach, we evaluated the

611   connection of these results with different functional diversity components: composition,

612   dominance, richness, divergence and evenness.

613   We show that the inclusion of a higher degree of functional diversity through the usage of a

614   trait-based approach plays a paramount role in the response of communities to disturbances.

615   The rainfall reduction was strong enough to functionally restructure communities in all of its

616   diversity components: communities with higher functional diversity also present a higher

617   ability to reorganize and adapt to a climatic change scenario because of its different

618   possibilities of response to the disturbance, while low functional diversity limits this

619   reorganization and adaptation.

620   However, despite the distinct impacts of drought on functional structure depending on the

621   modeling approach considered, the ability of storing carbon on an ecosystem level did not

622   present significant differences. It first highlights the need of the studies that seek to

623   understand ecosystem resilience to look beyond carbon storage (as is usually done). The

624   functional diversity of a community, and as a consequence, its capacity for reorganization

625   while undergoing change is fundamental for the long-term maintenance of the several

626   ecosystem processes that can be performed by a community (Mori et al., 2013).

627   In addition, like any modeling study, there are simplifications and assumptions that generate

628   caveats that are necessary to be taken into account. The first, and probably the most

629   important, is based on the fact that we have not used variant traits that are connected to

630   drought impacts on plant hydraulics, such as vulnerability to cavitation and embolism. This is

631   especially important considering that several studies have claimed that the decrease in carbon

632 storage due to drought is not, necessarily, linked to a decrease in carbon availability but much

633 more related to hydraulic failure (Eller et al., 2018; Doughty et al., 2015; Phillips et al., 2010;

634 Rowland et al., 2015). Also, our model do not consider the effects of changing functional

635 community to biotic interaction such as competition and facilitation, that seems to play a vital

636 role in determining ecosystem functioning (Mori et al., 2013). In that sense, we strongly

637 recommend that further studies using vegetation models, including CAETÊ, that aim to

638 understand the impacts of drought on carbon stock, should consider plant hydraulics and

639 biotic interactions.

640 In summary, the results presented here demonstrate that trait-based modelling approach

641 enables, as other vegetation models, the exploitation of the impacts of climate change in

642 biogeochemical variables but, beyond that, the impacts of these changes on functional

643 diversity and its different components. Thereby, it reinforces the idea that trait-based

644 modelling opens a space of questions exploration for functional and community ecology that

645 still remain under a thick layer of uncertainties such as community assemblage rules and the

646 functional diversity connection with ecosystem functioning.

647 **Acknowledgements**

651 **Data availability**

652 Model's code, as well as the results, can be found at

653 https://github.com/BiancaRius/CAETE_Rius_etal_2021.

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