

**Modeled changes on functional diversity and carbon storage driven by drought in the Amazon forest: a plant-trait vs. PFT-based comparison**

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**Abstract**

The drought impacts on functional diversity and how it modulates the Amazon carbon sink remain poorly understood, although evidences point that changes in functional richness, divergence and evenness can possibly change carbon stocks while keeping unchanged other ecosystem properties like vegetation structure. Here we investigate how a 50% reduction in rainfall can affect functional diversity and thereafter carbon stocks in the Amazon. We used two modelling approaches in which functional diversity is or is not predefined: one model version uses a plant functional type approach (PFTA; fixed trait values in 3 tropical PFTs) and the other uses a varying trait-based approach (TBA; semi-random combination of trait values creating 3000 plant life strategies). Six functional traits were considered as fixed/variant: carbon allocation and residence time on leaves, aboveground woody tissues and fine roots.

The imposed drought caused a widespread and similar magnitude loss of carbon storage in both approaches (~60%). Nevertheless, the geographical patterns of loss differed, with TBA showing more subtle changes along the basin, mainly on its southern limits. Also, the TBA presented an increase in fine roots investment (~10%), whereas the PFTA reduced carbon in all plant compartments. Changes in functional diversity were different in magnitude and direction between approaches: TBA(PFTA) showed changes, for fine roots allocation, of +19.33%(+4.94%) in richness; +276.54%(-74.71%) in evenness and -26.01%(+0.15%) in divergence, resulting in a functional reorganization of plant community allowing previously rare trait values to increase its density and a change in functional composition. Our results demonstrate that the inclusion of higher functional diversity did not show a significant difference in total carbon loss, mainly because the carbon assimilation processes (photosynthesis and respiration) did not differ between model versions. Notwithstanding, the different modeling approaches regarding carbon allocation and residence time suggest that varying-trait vegetation modeling offers a promising, though still underexplored, method to represent and better understand changing functional diversity and plant-trait distribution in light of biogeochemical processes that standard DGVMs do not allow.

**Keywords:** trait-based modeling, climate change, carbon allocation, functional composition, functional richness, functional evenness, tropical forest

## **Introduction**

The possible modification in Amazon forest's ability to absorb and store carbon due to climate change is permeated with uncertainties (Finegan et al., 2015), and the role of functional diversity (the values, ranges of values and relative abundance of functional traits in 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<sub>2</sub> 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<sub>2</sub> 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

selection for alternative functional structure, composition and diversity of forest community, modifications already observed in other studies (Enquist et al., 2015; Thompson, Mackey, McNulty, & Mosseler, 2009; Wieczynski et al., 2019). Functional diversity can be decomposed in three components: richness, divergence and evenness, that can respond differently to disturbances and that play different roles on plant communities. The rearrangement above cited together with modifications on functional diversity components can in turn affect the forest suitability and resilience to the new climatic conditions as has been shown in some observational studies (Aguirre-Gutiérrez et al., 2019; Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019).

The ability of the majority of DGVMs to capture such plant community rearrangement is very limited (Fyllas et al., 2014; Scheiter, Langan, & Higgins, 2013) since they commonly use the concept of plant functional types (PFTs) to represent vegetation (Reu et al., 2014; Scheiter et al., 2013; Verheijen et al., 2015). It means that the vegetation is represented in a very small, discrete, and *a priori* defined set of plant types. In that sense, the diversity of responses and the possibility for selecting alternative strategies that deal better with the new climate condition present very limited boundaries (Fyllas et al., 2014; Mori, Furukawa, & Sasaki, 2013). It possibly hampers advancements in the comprehension of the yet unknown effects of climate change in functional diversity and other ecosystem processes driven by or emerging from plant diversity (Díaz & Cabido, 2001; Lavorel & Garnier, 2002).

In order to overcome these limitations that a PFT approach imposes, some vegetation models - the so-called trait-based vegetation models - claim to represent plant trait diversity in a less discrete manner (Fyllas et al., 2014; (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013); Sakschewski et al., 2016; Scheiter et al., 2013). This type of vegetation model replaces the fixed parameters that represent functional traits in PFTs by variable ones (Pavlick, Drewry,

Bohn, Reu, & Kleidon, 2013; Reu et al., 2014; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010; Wullschleger et al., 2014), allowing a more functionally diverse representation of the responses of vegetation to a given environmental condition (Scheiter et al., 2013). It timely provides the opportunity for models to look beyond biogeochemical variables creating potential for exploring a multiplicity of functional ecology-related questions (Sakschewski et al., 2016; Davela-Filho et al., in prep.), many of them still unexplored, such as the role of the different components of functional diversity on resilience against environmental changes. Notwithstanding, the ability of trait-based models to effectively improve the representation of biogeochemical cycling and the representation of ecological processes that are commonly considered in standard DGVMs is yet to be assessed, as well as the comparative difference in the response of vegetation, in terms of functional diversity, to environmental changes when the trait-based approach is or is not considered.

In this article we employed a vegetation model applied for the Amazon region in a scenario of persisting drought. Two modeling approaches were used - one with low functional diversity (PFT approach) and one with high functional diversity (trait-based approach) - to investigate three main questions: (i) how do the modeling approaches differ in their results regarding the Amazon forest capacity to absorb and store carbon under the drought scenario?; (ii) what is the drought impact on the different components of functional diversity for both modeling approaches?; and, finally, (iii) what is the role of the functional diversity level and the impacts of drought on it to the response of the two modeling approaches regarding the carbon storage?

## **Materials and methods**

### *The CAETÉ 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.

The environmental filtering mechanism acts in the model such that each PLS within the trait space performs differently under the same environmental conditions (e.g. temperature and precipitation; Diaz, Cabido, & Casanoves, 1998; Webb et al., 2010). All grid cells are initiated with the same set of PLSs (number and identity) in a condition analogous to a bare soil. Therefore, even though all trait combinations are equally probable to occupy a given grid cell and each of them has its particular climatic occurring space, it is expected that some PLSs will survive and present different performances and abundances (percentage occupation of the grid cell weighted by their biomass; Appendix A.3.1) and some of them will perish in the first simulation steps. PLSs that do not survive are excluded from the grid cell (and cannot be reestablished in that grid cell in this model version).

The differential survival and abundance between PLSs are made possible because each functional trait in the model is related to at least one trade-off (cost-benefit relationship) leading to different relative performances and ability to deal with the environment. The trade-offs also prevent the model from creating the so-called “Darwinian demons” (i.e. maximizing all the functions that contribute for fitness; Scheiter et al., 2013). Since functional traits both respond to and affect ecosystem-level processes (Díaz et al., 2013; Funk et al., 2017; Lavorel & Garnier, 2002) the varying PLSs ecophysiological performance generates heterogeneous biogeochemical fluxes and stocks and functional diversity through space and time. Such model outputs are aggregated to the grid cell scale according to the modeled abundances of PLSs, which are determined on the basis of the biomass-ratio hypothesis (Grime, 1998). A table with each functional trait and its respective trade-off and equation can be found in Table A.3. An in-depth description of the CAETÉ model can be found in Appendix A.3.

### *Simulation setup*

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 compartment (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).



Three tropical PFTs were defined in the PFTA to describe the vegetation and the parameters that represent the functional traits used for this study are *a priori* defined following previous literature (Table A.1). The use of only tropical PFTs is justified given the study area (Amazon forest), and with them, we tried to encompass the majority of PFTs previously used in standard DGVMs for this region. In the trait-based model approach, the initial range of values for each functional trait (from where some of them will be sampled to create the hypervolume) are indicated in Table A.2. The ecophysiological processes linked to each functional trait, its trade-offs, and associated formulations are summarized in Table A.3 and described in Appendix A.3.2. It is important to highlight that CAETÊ admits the use of any functional trait of interest, as well as any number of them, as long as the trait is linked to existing model formulation and can have trade-offs implemented. CAETÊ works in a spatial resolution of 0.5° x 0.5° and is coded mainly in Fortran 90 with some modules written in Python.

#### *Input data*

The following climatic data were used as inputs for the model: air surface temperature, precipitation, shortwave radiation, relative humidity and atmospheric CO<sub>2</sub> concentration. The first three variables were obtained from mean monthly data for the period between 1980 to 2010. These data are available in the Inter-Sectoral Impact Model Intercomparison Project 2 (ISI-MIP2; Warszawski et al., 2014). Atmospheric CO<sub>2</sub> concentration was obtained from the National Oceanic and Atmospheric Administration platform (<http://co2now.org/images/stories/data/co2-mlo-monthly-noaa-esrl.pdf>), using the mean value of [CO<sub>2</sub>] for the same period of the climatic data (1980-2010).

#### *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<sup>1</sup> 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 <sup>1</sup> Here, functional trait space is the total range of values for a specific functional trait.

240 For multi-trait functional diversity we used the hypervolume metric following Blonder et al.  
241 (2014). Hypervolumes can combine the distribution of  $n$  trait values and then calculate  
242 functional diversity components (Barros et al., 2016; Blonder et al., 2018), for example, the  
243 volume size, that indicates how much of the possible functional space an ecological unit  
244 occupies (i.e. the variance of values; Barros et al., 2016), that can be interpreted as functional  
245 richness. Also, the distribution of values within the hypervolume informs, together with the  
246 centroid (that indicates the mean values), about system functional composition.

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

#### 258 *The role of functional diversity on ecosystem response to environmental change*

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

drier climate in its ability to store and partition carbon compared to a community with lower functional diversity (PFT approach). For this we compared the degree of change in carbon stock either considering the whole plant or the compartments separately. To complement this analysis, we looked into the underlying mechanisms that generate the difference of response by exploring the effects of drought on functional diversity and composition *per se* (see next section).

#### *Functional composition and diversity response to drought*

For the single-trait framework analysis, we compared the TPDs generated by the two climatic conditions for all the six traits: regular climate and reduced precipitation. For this, the dissimilarities between the two TPDs were computed by calculating the degree of overlap between the two distributions (dissimilarity index that can vary from 0 – completely functionally similar - to 1 – completely functionally different; Carmona, de Bello, Mason, & Lepš, 2016). This index shows if functional structure of the community was significantly modified by the climate scenario (Carmona, de Bello, Mason, & Lepš, 2019). We also compared how the three facets of functional diversity aforementioned changed after the applied disturbance.

For the multi-trait framework four hypervolumes were constructed and compared: one with regular climate and other with reduced precipitation for each of the modeling approaches. After performing the PCA (a previous necessary step explained in section *Representation of functional diversity and composition*) the hypervolumes were delineated using the factor scores of the three first principal components (PCs) since they were able to explain more than 98% of the variance. It is important to highlight that we needed to calculate the PCA with 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 in 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.

## 294 **Results**

### 295 *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.

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.

331 Nevertheless, the change in functional composition was different when comparing the  
332 modeling approaches. First, considering all the traits, the PFTA showed a trimodal  
333 distribution, with three clear and discrete peaks along the trait space when the precipitation is  
334 reduced, while in TBA the distribution showed a higher diversity of values that had their  
335 density increased, resulting in a much more diffuse distribution within the functional space.  
336 This pattern can also be seen when considering all traits together through the hypervolumes:  
337 for the PFTA it is possible to observe three clear data grouping under drought (Figure 4a), and  
338 a much less discretized data distribution from the TBA (Figure 4b). Also, for the TBA it is  
339 important to observe that the increase in the trait values density is more prominent for the  
340 ones that were previously rare under the regular climate conditions (Figure 3a-c and g-i). In  
341 that sense, the TBA showed a clear pattern with reduction in precipitation for traits related to  
342 allocation: an increase in density toward higher values of carbon in fine roots and an increase  
343 in density toward lower values of carbon in leaves and especially in ABGW. On the other  
344 hand, the PFTA showed a much smaller change, and changes in density values were restricted  
345 to a small area of the functional space, with almost no change in the range of values (Figure  
346 3d-f and j-l). A similar pattern of density distribution change was found for the residence time  
347 traits: the PFTA showed an increase in residence time for leaves and fine roots (despite the  
348 very slight change) and a conservation in residence time values for ABGW, while for TBA  
349 we observed an increase in residence time for leaves and fine roots but a decrease for ABGW.

#### 350 *Functional diversity under drought scenario*

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

nonetheless, in the PFTA traits showed a decrease in this functional diversity component and in a lower degree of change (74% maximum). As a whole, the TBA traits presented reduction in divergence, while the opposite result was observed for the PFTA, also with the same pattern found for the other functional diversity facets regarding the magnitude of change.

Also, with the applied drought scenario, the hypervolumes for TBA and PFTA showed a pronounced change. (Figure 4; see movie SM.1 for a 3D animated representation) Under natural climatic conditions the size of the volume that the data occupy was equal to 1.711 and 0.007 for TBA and PFTA, respectively; while under reduced precipitation the volume size increased for both approaches: 47.837 for the former and 0.755 for the latter. It indicates an increase in the occupation fraction of the functional space under a drier climate (i.e. increase in the amplitude of trait's variation and richness) in a magnitude of 2,695.0% for the TBA and 1,025.0% for the PFTA. The overlap degree between hypervolumes (before and after the drought scenario) yielded a value of 0.038 for the TBA and of 0.009 for the PFTA, indicating almost no similarity of the hypervolumes. Finally, the distance between the centroids of the two hypervolumes after imposed climatic change indicates the change in the mean values: the centroid distance in the TBA was 5.25 and 0.937 in the PFTA (i.e. the mean values were modified in a higher magnitude for the former approach).

## Discussion

Briefly, our results showed:

- PFTA and TBA presented a similar magnitude decrease in total carbon storage 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 the 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)

ecosystem tends to be more resilient to environmental changes (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019). However, the similar C loss magnitude can be partially explained by the fact that the carbon assimilation processes (photosynthesis and respiration) were not modified between the two modelling approaches and some important processes (e.g. embolism) and functional traits linked to drought response are still not included in the model (in the *Discussion* section some caveats are presented).

Nevertheless, despite the similar magnitude in total carbon loss, the two approaches presented differences on the geographical pattern of loss: the model approach with high initial functional diversity (TBA) was able to maintain carbon in regions where the other approach with low initial functional diversity (PFTA) lost it completely, especially in the southern and central parts of the Amazon forest, even though the former lost carbon in a higher degree than the second where both modeling approaches maintained carbon. This result at first may seem contradictory, but can be explained by the fact that the mechanisms that underlie ecosystem carbon loss was different between the approaches: while the PFTA showed, on average, almost no change in the carbon partitioning with drought, the TBA increased the investment in fine roots to the detriment of the investment in leaves and ABGW. It is well known that climatic changes, such as drought, induce changes on C partitioning patterns (Doughty et al., 2014; Kannenberg et al., 2019) including a prioritization of root investment at the expense of other tissues (Doughty et al., 2014; Phillips et al., 2016; Rowland et al., 2014). In our model, a higher investment in fine roots increases the uptake of water, which makes the community better able to deal with drought and maintain carbon stocks or reduce the degree of loss. We observed it in the TBA: an avoided of total carbon loss in grid cells where the PFTA was not 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

reorganization is supported by the dissimilarity values found between traits distributions before and after the disturbance both in the single-trait and multi-trait analysis.

These results are in agreement with theoretical, experimental and modeling evidences that show environmental change is able to cause a modification on functional structure (Enquist & Enquist, 2011; Hillebrand, Bennett, & Cadotte, 2008; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011), dominance (Hillebrand et al., 2008; Schmitt et al., 2019; Valencia et al., 2015), composition (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007) and diversity components (Hillebrand et al., 2008; Zhang, Chen, & Reich, 2012). In our simulations these changes occurred because the environmental filtering was modified and, as a consequence, the selection of the strategies changed towards favoring trait values that were previously rare or absent. Those changes modified the abundance of traits and the way that communities occupy the functional space (Carmona, de Bello, Mason, & Lepš, 2016, 2019; De Bello, Carmona, Mason, Sebastià, & Lepš, 2013; Enquist & Enquist, 2011). Next sections explore the changes related to functional dominance, composition and diversity components.

#### *Changing functional dominance*

The differential occupation of the functional space with drought was specially caused by the change in dominance: an expressive decrease in abundance of a narrow range of trait values to a wider one for all the considered traits, especially for the TBA. Dominance reflects the distribution of traits in a community and plays a fundamental role on ecosystem processes, such as carbon cycling (Cavanaugh et al., 2014; Ruiz-Jaen & Potvin, 2011), since, theoretically, the dominant traits contribute more to aggregate processes in communities and 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<sup>2</sup> 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 <sup>2</sup> Diversity of responses that traits or trait combinations show to disturbances in a given  
3 community (Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016)

range of values prior to the imposed climatic change. That means the TBA was able to select strategies that coped better with the drought scenario by increasing fine roots allocation and residence time, since this tissue is strictly related to the water uptake; likewise, the increase observed in residence time for leaves in this employed approach, despite the decrease in allocation, can be identified as a mechanism to maintain the levels of photosynthesis since the reduction of allocation for this organ reduces total photosynthetic rates for a given plant strategy.

In fact, literature shows that carbon partitioning can exhibit plasticity depending on water availability (Bazzaz, 1991; Franklin et al., 2012; Weiher et al., 1999; Weiner, 2004). According to the optimal partitioning theory, the preferential allocation should be directed towards the organ responsible for the acquisition of the most limited resource, in that sense, one should expect, as observed in the TBA results, an increase towards roots investment under water limitation (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972). However, the fate of carbon under drought conditions is still a matter of debate, and conflicting results are found in literature (Hofhansl, Schnecker, Singer, & Wanek, 2015; Litton, Raich, & Ryan, 2007) but some pattern can be identified: apparently a mild drought, or stronger dry seasons, lead to a higher investment in fine roots (Blessing, Werner, Siegwolf, & Buchmann, 2015; Brando et al., 2008; Doughty et al., 2014; Lacoite, 2000; Rowland et al., 2014), while a more persistent and severe drought could decrease allocation belowground followed by a higher investment in wood and canopy tissues (Blessing et al., 2015; Sevanto & Dickman, 2015). The investment in wood tissues could be explained by the fact that these organs maximize plant hydraulic safety (Hofhansl et al., 2015).

In that sense, it seems that the impact of drought on allocation is not straightforward and may depend on a series of variants that goes beyond carbon partitioning such as the duration,

severity of drought and other plants features like the sensitive to embolism and cavitation, not yet addressed in the employed model formulation.

Comparing our results about the change in functional composition with other studies can be tricky, once the result of studies regarding changes in functional composition is highly dependent on the chosen traits. For example, Esquivel-Muelbert et al., (2018) and Aguirre-Gutiérrez also found an increase in abundance of plants of the trait values of which confers them a higher tolerance to drought. Despite of this obstacle in comparing the results, it is undeniable that our employed TBA is able to at least identify this type of community level change, and a promising next step is to include hydraulic, leaf and wood traits that has been shown to be crucial to understand the response of ecosystems to drought (Barros et al., 2019; Christoffersen et al., 2016; O. L. Phillips et al., 2010; Poorter et al., 2010). Our findings related to functional traits composition become fundamental by allowing advances on the still undergoing question of how functional shifts moderate drought-induced biomass loss and forest resilience against environmental change.

#### *Functional diversity facets responses*

Few studies have explored how drought impacts the (Carmona, de Bello, Mason, & Lepš, 2016) different functional diversity components, despite the known importance of them for ecosystem functioning and resilience (Carmona et al., 2016). Here we explored, for the first time, the impact of drought on Amazon functional diversity considering its three primary components: richness, evenness and divergence, and also examined functional diversity considering all the six chosen functional traits together.

The observed impacts on functional diversity, for both modeling approaches, were a reverberation of the community functional reorganization, especially the dominance change.



For functional richness we observed an increase in this variable for the two modeling approaches but the magnitude of change was much higher for the TBA, what is highly connected to the fact that the latter presents a wider range of possible values to occupy the space, while this range is very limited for the former. It also reflected on the volume occupied in the functional space considering the traits altogether: volume increases in both the approaches, but the TBA showed an increase more than two fold stronger when compared to the PFTA. This is contrary to the hypothesis that a harsher environment would decrease functional richness by selecting a narrow range of strategies due to the environmental filtering (Cornwell et al., 2006; Funk et al., 2017; Kleidon, Adams, Pavlick, & Reu, 2009; Perronne & Gaba, 2017). However, the observed functional reorganization is able to explain this unexpected result, since they allowed new combinations of traits to establish or increase their occurrence (Mouillot et al., 2013). It means that, in some cases, functional richness can increase in disturbance scenarios if the environmental change affects mainly the dominant strategies or trait values.

Regarding evenness: the increasing evenness in the six functional traits observed for the TBA means that the drought scenario made the distribution of trait values in the trait space to become more regular. On the other hand, the PFTA showed a decrease in this functional diversity component for the majority of traits. The evenness increase in TBA is tightly related to the observed decrease of dominance and increase of abundance of trait values that were very rare before the disturbance. The decrease in evenness for PFT approach can be explained by the fact that the reduced precipitation decreased the dominance of a very restricted range of trait values (dominance of one PFT) and allowed the occurrence of the other 2 PFTs. Since the difference between the PFTs is very discretized, the occurrence of trait values ended up concentrated in three peaks of density hence turning the distribution less even. Evenness can

also be interpreted as an evidence of the effectiveness in using the functional niche space: the higher the evenness, the higher the utilization of the total functional space (De La Riva et al., 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011). Therefore, our results indicate that a change in the environment can force the community to better occupy the functional niche space, if it presents a sufficient variability in its trait values, as we observed for the TBA.

Lastly, the TBA presented a general decrease in divergence while the PFTA approach showed an increase for this functional diversity facet. The decrease in divergence found for TBA means that, regarding a specific trait, the values distribution is no longer concentrated in only one extremity of the functional space, but other trait values that were not that important before became significant for the community and for the ecosystem functioning with the environmental change. Beyond that, divergence is also a way to understand if the frequency distribution of trait values in the functional niche space maximizes the total community variation in functional characters (Mason et al., 2005). In that sense, low divergence could be a result of different, or even contrasting, strategies being able to deal with the new conditions (Funk et al., 2017). The increase in divergence found in the PFTA is a product of the emergence of the three peaks on traits distribution. For this approach a better occupation of functional space (low divergence) is impossible considering its very low diversity of trait values available.

## *Conclusions*

In this study we aimed at understanding the role of functional diversity on the ability of Amazon forest to store carbon under a persistent drought scenario (50% homogeneous 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

storage due to drought is not, necessarily, linked to a decrease in carbon availability but much more related to hydraulic failure (Eller et al., 2018; Doughty et al., 2015; Phillips et al., 2010; Rowland et al., 2015). Also, our model do not consider the effects of changing functional community to biotic interaction such as competition and facilitation, that seems to play a vital role in determining ecosystem functioning (Mori et al., 2013). In that sense, we strongly recommend that further studies using vegetation models, including CAETÊ, that aim to understand the impacts of drought on carbon stock, should consider plant hydraulics and biotic interactions.

In summary, the results presented here demonstrate that trait-based modelling approach enables, as other vegetation models, the exploitation of the impacts of climate change in biogeochemical variables but, beyond that, the impacts of these changes on functional diversity and its different components. Thereby, it reinforces the idea that trait-based modelling opens a space of questions exploration for functional and community ecology that still remain under a thick layer of uncertainties such as community assemblage rules and the functional diversity connection with ecosystem functioning.

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## **Data availability**

Model's code, as well as the results, can be found at [https://github.com/BiancaRius/CAETE\\_Rius\\_etal\\_2021](https://github.com/BiancaRius/CAETE_Rius_etal_2021).

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