**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 evidence point that changes in functional richness, divergence and evenness can possibly change carbon stockswhile 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 otheruses 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 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 explored (Poorter et al., 2015; Sakschewski et al., 2016; Sitch et al., 2008)⁠. Dynamic Global Vegetation models (DGVMs) have been widely used to explore the question from a biogeochemical perspective (Cramer et al., 2001; Scheiter, Langan, & Higgins, 2013) providing substantial contribution to our current knowledge of the Amazon forest ecology and resilience (Díaz & Cabido, 1997; Prentice et al., 2007; Scheiter, Langan, & Higgins, 2013). For instance, the projected possibility of a large-scale degradation of the Amazon forest driven by severe climatic changes (Cox, Betts, Jones, Spall, & Totterdell, 2000)⁠ and the role of soil phosphorus as a limiting factor to CO2 fertilization in the region (Fleischer et al., 2019), are all results derived out of studies using DGVMs.

Nonetheless, the results of DGVMs regarding to the future of Amazon forest’s carbon stock are contradictory and diverge both on the magnitude and on the direction of change (Huntingford et al., 2013; Powell et al., 2013; Rammig et al., 2010)⁠. The different climatic scenarios, parameterization and model formulation (e.g. nutrient limitations to CO2 fertilization) may be some possible reasons for such a degree of uncertainty (Huntingford et al., 2013; Quillet, Peng, & Garneau, 2010; Sitch et al., 2008; Verheijen et al., 2015)⁠.

Additionally, the poor functional trait diversity represented in DGVMs in the tropics is another feature that can potentially lead to inaccurate estimates of the impacts of environmental changes on ecosystems, especially in hyperdiverse (at least in the taxonomic sense) ecosystems such as the Amazon forest (Aguirre-Gutiérrez et al., 2019)⁠ . This is because it is reasonable to expect alterations on the environmental filtering following climatic changes, and hence, the requirements for an individual to be successful may change as well (Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010)⁠⁠. It implies that the physiological tolerances determined by functional traits are also modified, possibly generating a 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 evennes, 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 on 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; Darela-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 to 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 to the carbon storage?

**Materials and methods**

*The CAETÊ model: an overview*

As a trait-based model, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model focus on representing a higher variability of plant functional traits and, whenever possible, the range of functional diversity found in plant communities. As such, vegetation is represented by a set of functional strategies (called as plant life strategies, PLS), being that each of which is a unique combination of functional traits values. The combination of such trait values describes the ecophysiological behavior of plants and their relationship with the environment. These traits control, for example, the differential acquisition of carbon, light and water, ultimately defining how the strategy copes with the environment and, together with the other PLSs of the community, determine ecosystem functioning (Figure 1).

The underlying premise to create these PLSs is that the range of values of a functional trait observed in nature can be regarded as one axis of a multidimensional hypervolume formed by the combination of *n* chosen functional traits (Blonder, 2017; Villéger, Mason, & Mouillot, 2008)⁠. In that sense, each point inside of this hypervolume is a unique combination of values for each of the functional traits, a PLS. The volume that all points together occupy can be seen as a functional trait space. The values of functional traits that compose the hypervolume are semi-randomly sampled from the complete range of values (to more details see Appendix A.1). The combination of all sampled values generates a large number (>105) of combinations within the functional space. As for other trait-based models (e.g. Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Reu et al., 2011), CAETÊ follows the assumption that sampling an appropriate number of PLSs from the potential functional space (see sensitivity test in Appendix A.2) combined with an environmental filtering mechanism together with a representation of competition allow the model to produce reasonable biogeochemical and 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 tough 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 CAETÊ model can be found in Appendix A.3.

*Simulation setup*

In this study we employed, for the Amazon basin, a non-dynamic version of the CAETÊ model, which calculates equilibrium solutions based on long-term mean monthly climate variables (for the period between 1980 and 2010). A spinup simulation period of ????? years was carried out to initialize carbon stocks in different plant compartments (see Appendix A.3.4).

Two sets of models runs were carried out: one employing, as the majority of current vegetation models, a PFT approach (with a low functional diversity initialization: 3 PFTs) and the other using a trait-based approach (with a high functional diversity initialization: 3000 PLSs). Despite the difference in the number of plant types and in the way that functional traits values are chosen, the general model formulations and principles are the same for both model approaches.

Since our focus of analysis here is on the process of carbon storage, we set the functional traits related to the percentage of the carbon distributed to plant compartments (carbon allocation) and the carbon residence time in each plant compartiment (how long the carbon stay in each compartment) to be variable between PLSs/PFTs. Plants are split into three compartments: leaves, aboveground woody tissues (hereafter ABGW) that represents stem and branches, and fine roots; hence, six functional traits are considered as variable: the allocation and the carbon residence time for each of the plant compartments. Together, these functional traits ultimately define the amount of carbon in each compartment of a PLS or PFT at each time step, and are of primary importance for determining absorption and storage of carbon in the whole study area (Chambers, Fisher, Hall, Norby, & Wofsy, 2012; Fatichi & 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 previsously 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 0.5º x 0.5º 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 CO2 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 CO2 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 [CO2] for the same period of the climatic data (1980-2010).

*Representation of functional diversity and composition*

Here we focused in a large-scale analysis of functional diversity for the whole Amazon basin, in opposition to a detailed grid cell-by-grid cell analysis. In that sense, the value of each of the six variant functional traits in each grid cell is represented by a mean value that is estimated according to the relative abundances of PFT/PLSs (see Appendix A.3.1) using the Community Weighted Mean (CWM) metric (Díaz et al., 2007; Grime, 1998)⁠.

Additionally, functional diversity is regarded here both from the perspective of its single-trait components as well as its multi-trait component (i.e. the combination of traits). The single-trait element allows to interpret more precisely how the different traits interact (affects and responds) with the environment (Lepš, de Bello, Lavorel, & Berman, 2006; Ricotta & Moretti, 2011)⁠, while the multi-trait component gives information about the ecological strategy as a whole (i.e. as a syndrome), incorporates the relations between the traits, including its trade-offs, and also how the community occupies the given possible functional space (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016; Blonder, Lamanna, Violle, & Enquist, 2014)⁠⁠.

We considered that single-trait functional diversity can be decomposed in three components following Carmona et al. (2016) definitions and methods: (i) functional richness: the portion of the total functional trait space[[1]](#footnote-2) that is occupied in an ecological unit derived from the variance of trait values of all the considered organisms (PFT/PLSs in our case); (ii) functional evenness: how regular is the density distribution of the PLSs’ or PFTs’ trait values in the functional trait space; (iii) functional divergence: the degree to which the abundance of PFT/PLSs’ trait values are distributed towards the extremes of their functional trait space. Carmona’s method uses probability density distributions for the calculation of the components, the so called TPD’s (trait probability distribution).

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. Additionaly, the PCA indicates the trade-offs that emerges 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 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 on 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)⁠; after that, separate hypervolumes were calculated from the factor scores corresponding to each climatic condition and model approach dataset. After constructing the four hypervolumes we were able to compare them in terms of size (richness), the distance between the centroids (to verify the change on mean values) and the degree of overlap through Jaccard similarity index that range from 0 (completely dissimilar) to 1 (completely similar). These three metrics together can give us an idea of the magnitude of change in functional diversity and composition with drier climate considering plant ecological strategies as a whole.

**Results**

*Drought impacts on carbon storage and partitioning*

The reduction in precipitation caused a considerable basin-wide reduction of carbon stocks both for the high and low degrees of functional diversity employed in the model: -57.48% and -57.45%, respectively. Also, for both approaches this reduction was higher in regions with naturally lower precipitation levels, mainly in southern, central and northern parts of the basin (Figure 2a and 2b). However, the spatial pattern of carbon loss driven by the imposed drought condition differs between the trait-based (hereafter TBA) and PFT approaches (hereafter PFTA). The TBA was able to maintain carbon in some areas where the PFTA has lost it completely. This is more evident in naturally drier areas, such as the transition between the Amazon forest and the savannah (*cerrado*) and central Amazon. It is noteworthy also that the loss of carbon in TBA is more gradual, i.e., there is a smoother gradient between a grid cell value and its neighboring cells, and also across different basin regions. On the other hand, in the PFTA the carbon loss is more abrupt both between neighboring cells and across the regions of the basin.

Despite the similar magnitude in the total carbon storage change, specific plant compartments have shown different patterns of changes when comparing the two approaches (Figure 2c and 2d for fine roots and Figure SM.2 for leaves and ABGW). None of the compartments has shown, for any area, an increase in carbon stock with drought, except for the fine roots compartment in TBA, indicating a change on carbon partioning for the latter approach. This increase, around 10% (blue areas in Figure 2d), was observed in the transitions from humid and evergreen forest to the Brazilian savannahs (*cerrado*) and also in the basin northwest. Even in areas where the root compartment has lost carbon in the TBA, it was in a lower degree when compared to the other compartments and to the PFTA approach.

*Functional composition under a drier climate*

The applied drought scenario caused a modification on the density distribution of the six variant functional traits both for PFTA and for TBA (Figure 3). For all the traits, the shape of the curve changed considerably, reflecting on the dissimilarity index: all of them presented a dissimilarity approximating to 1, which means that they became functionally different with the new climatic condition (Table 1). For example for all of them, the maximum values of the probability density distributions were lower under low precipitation, i.e., the peak of the curves decreased, meaning that there was a clear and strong reduction in dominance for the communities under drought. Because of the observed decrease in dominance other trait values that were previously rare (i.e. very low density), or absent, were able to occur in the trait space or increased their density, changing the shape of the curves, which ultimately demonstrates a change in the functional composition of the communities and on the different components of functional diversity.

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 on 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, 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 to 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 on 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 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 investiment in this tissue;
* Both modelling approaches presented changes on the three facets of functional diversity, however the magnitude of thechange 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 processess (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 underlies ecosystem carbon loss was different between the approaches: while the PFTA showed, on average, almost no change on 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 rearrangement while the PFTA could not (the discussion of the reason is presented in the next section).

The shift in carbon partitioning due to climate is of primary relevance for the future of Amazon carbon stocks (Doughty et al., 2015; Friedlingstein et al., 2006)⁠ and is especially important if the carbon is allocated towards pools with shorter turnover, such as fine roots or even root exudates (Jiang et al., 2020)⁠, that contribute in a lesser extent to total carbon biomass comparatively with other pools such as wood tissues (Chave et al., 2009; De Kauwe et al., 2014; Kannenberg et al., 2019; Luo, 2003)⁠. Our modeling exercise captured well this process: the drought lead to an increase in investment of fine roots in the TBA that provided greater resistance to drought, preventing the total loss of carbon in several grid-cells, and also caused a lower carbon storage in other tissues, mainly on ABGW and led to a relative lower carbon storage in some locations when compared to the PFTA. In that sense, if the ability to store carbon is used as the only proxy for ecosystem resilience, as is commonly used, (e.g. Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016), it may result in inaccurate interpretations about the response of tropical forests to climate change.

Lastly, since model formulation was equal in the two approaches, one can conclude that the differences observed regarding to carbon storage are derived from the initial functional diversity employed and from the changes that the imposed climatic scenario caused on different components of functional diversity.

*Forest functional reorganization*

Our results show that the applied long-term drought scenario caused a significant functional community reorganization of Amazon forest in terms of composition, dominance relationship, 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)⁠.

The dominance change modeled in our study and observed/theorized in the other studies cited above, is in agreement with the theory that the shift in community dominance with a change in climate could be caused by a compensatory dynamic process, also called as ‘functional density compensation’: when the composition of an ecosystem adjust to the new conditions enabling types of plants (or trait combinations, in our case) that previously exerted a less relevant functional role (i.e. low density) to increase their dominance and vice-versa (Gonzalez & Loreau, 2009; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016)⁠. As a consequence, the diversity of traits values available in a community is central, since it can act as an “insurance” for new environmental conditions (Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999)⁠. It also reinforces the importance of rare trait values, functional strategies or species, for the maintenance of ecosystem processes in future environmental conditions, including tropical forests that commonly present a hyperdominance of species with specific functional traits (Cornwell, Schwilk, & Ackerly, 2006; Jain et al., 2014; Mouillot et al., 2013; van der Sande et al., 2017).⁠

Such a functional density compensation phenomenon was well captured in our modeling results: reduced precipitation led to a consequent emergence of new strategies and/or increase in abundance of previously rare trait values occurrence. However, the capacity of a community to promote a compensatory dynamics strongly depends on its functional diversity (Mori et al., 2013)⁠⁠. This was clearly demonstrated in our work when comparing the PFTA and the TBA. The functional space occupation as a consequence of the decrease in dominance was different for the approaches, for example, the PFTA presented, for all traits, a restricted possibility of the occurrence of new trait values, presenting trimodal curves with drought. On the other hand the trait-based approach showed a more spread occupation of the functional space. This was also observed in the multi-trait analysis of functional diversity: the wider occupation of the functional space with the reduced precipitation was much stronger in the TBA when compared to the PFTA, as well as the centroid distance.

These contrasting results are due to the modeling approach-dependent difference in the response diversity[[2]](#footnote-3) that was imposed by the level of functional diversity in which the model was initialized. Such a response diversity was very limited for the PFTA since it was provided with only 3 possibilities of trait combinations, preventing better suited traits combination to establish themselves under the new climatic conditions whereas the TBA was provided with 3000 possible trait combinations. It also explains why the carbon partitioning rearrangement was so limited for the PFTA.

Also, the different diversity of responses within the approaches can explain the geographical contrasts in the carbon loss. The smoother loss of carbon observed in the TBA was possible because of its higher capacity of functional reorganization due to response diversity, selecting better suited trait combinations in accordance with the grid-cell environment. Meanwhile, the PFTA presents a reorganization very restricted because of its low diversity of responses and the change of environmental conditions between one grid cell and another could not be suitable for the 3 available trait combinations.

*Changing functional composition*

In the present study the different employed modeling approaches presented distinct responses in terms of changes in community composition, which are mainly associated to the magnitude of the change: while the change in the occupation of the functional space for the TBA showed a prominent shift in allocation towards fine roots, in the PFTA the composition change is much less remarkable, with the maintenance of the more abundant traits around the same 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; Lacointe, 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 on 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 on 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 to 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 functional diversity (low and high, PFT and trait-based respectively). In order to understand the mechanisms that underlies the observed responses of each approach, we evaluated the connection of these results with different functional diversity components: composition, dominance, richness, divergence and evenness.

We show that the inclusion of a higher degree of functional diversity through the usage of a trait-based approach plays a paramount role on the response of communities to disturbances. The rainfall reduction was strong enough to functionally restructure communities in all of its diversity components: communities with higher functional diversity also present a higher ability to reorganize and adapt to a climatic change scenario because of its different possibilities of response to the disturbance, while low functional diversity limits this reorganization and adaptation.

However, despite the distinct impacts of drought on functional structure depending on the modeling approach considered, the ability of storing carbon on an ecosystem level do not presented significant differences. It first highlight the need of the studies that seek to understand ecosystem resilience to look beyond carbon storage (as is usually done). The functional diversity of a community, and as a consequence, its capacity for reorganization while undergoing change is fundamental for the long-term maintenance of the several ecosystem processes that can be performed by a community (Mori et al., 2013).

In addition, like any modeling study, there are simplifications and assumptions that generates caveats that are necessary to be taken into account. The first, and probably the most important, is based on the fact that we have not used variant traits that are connected to drought impacts on plant hydraulics, such as vulnerability to cavitation and embolism. This is especially important considering that several studies have claimed that the decrease in carbon storage due to drought is not, necessarely, 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 on biogeochemical variables but, beyond that, the impacts of theses 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.

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1. Here, functional trait space is the total range of values for an specific functional trait. [↑](#footnote-ref-2)
2. Diversity of responses that traits or trait combinations show to disturbances in a given community (Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016)⁠ [↑](#footnote-ref-3)