**Accounting for trait variability in vegetation models enhances future projections of Amazon forest plant functional diversity and carbon storage**

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**Abstract**

The impacts of projected reduced precipitation and other climatic changes on functional diversity and how its different components (richness, evenness, divergence and composition) modulates the Amazon carbon sink remain underexplored and therefore poorly understood. Here, we present a unique trait-based approach, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model. We first evaluate CAETÊ’s performance in comparison to remote sensing and *in situ* estimates of vegetation carbon storage and net primary productivity (NPP) for the Amazon basin. Furthermore, we applied a 50% precipitation reduction scenario to assess how projected climate change might affects functional diversity and associated carbon stocks across the Amazon. We used two modeling approaches to represent functional diversity: (i) using three plant functional types (PFTA) with fixed trait values, and (ii) applying a varying trait-based approach [TBA; semi-random combination of trait values creating 3000 plant life strategies (PLSs)]. Six functional traits were considered to build up the plant life strategies for TBA and the PFTs for PFTA: carbon allocation and residence time on leaves, aboveground woody tissues and fine roots. Our results showed that the inclusion of trait-variability (TBA) improves model perfomance in representing NPP and vegetation carbon stocks. Beyond, we found that TBA, compared to PFTA, presented a higher ability to functionally reorganize with disturbance through changes in abundance of the PLSs present in the community thanks to the diversity of possible responses. On the other hand, the use of a few PFTs overestimated the impacts of environmental changes because of its limited capacity to reorganize. The higher TBA ability to functionally reorganize allowed the community of this modeling approach to better occupy the functional space through the changes in functional diversity components (increase in richness and evenness and decrease in divergence). It created new functional niches and enabling new trait combinations, or previously rare, to compose the community. We observed, for example, an abundance increase of PLSs with higher investment in fine roots investment to deal with the lower water availability in the TBA, what turned the community more resilient. Our findings highlight that accounting for trait variability in vegetation models allows more accurate projections of ecosystem processes under current and future scenarios. Moreover, it allows the advance on the understanding of biodiversity-ecosystem functioning relationship by showing for example that the use of carbon storage as the only proxy for ecosystem resilience may result in limited interpretations about the response of ecosystems to climate change bringing out the importance of the still neglected role of functional diversity components**.**

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

**Introduction**

It is projected, for the 21st-century, that the Amazon forest will experience more frequent and more extreme moisture stress (Duffy, Brando, Asner, & Field, 2015; Esquivel-Muelbert et al., 2017; Hubau et al., 2020; Lewis et al., 2011)⁠, which can directly impact vegetation carbon storage (da Costa et al., 2010; Hubau et al., 2020; Phillips et al., 2010)⁠ and induce biodiversity shifts, including changes in functional diversity - the values, ranges of values and relative abundance of functional traits in a given community or ecological unit (Díaz et al, 2007) - (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Zhang, Niinemets, Sheffield, & Lichstein, 2018)⁠. All of these changes, which can be caused by reduced precipitation, have been already observed in Amazon forest long-term inventory plots (Esquivel-Muelbert et al., 2018, 2017)⁠, as well as, ecosystem-scale field experiments (Meir et al., 2009; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007; Rowland et al., 2015)⁠, conducted in other tropical regions (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012)⁠. However, the degree and direction (increase or decrease) to which associated ecosystem process, such as vegetation carbon storage, will be affected, remain uncertain (Bonal, Burban, Stahl, Wagner, & Hérault, 2016; Hubau et al., 2020; Yang et al., 2018). Despite of major and continuing efforts to describe and explore crucial ecosystem processes in hyperdiverse tropical forests [*e.g.* RAINFOR (The Amazon Forest Inventory Network); AfriTRON (The African Tropical Rainforest Observation Network); PAN-AMAZONIA (Project for the Advancement of Networked Science in Amazonia)], both the role that functional diversity plays in maintaining crucial ecosystem processes, such as vegetation carbon storage, and the impact of projected climate change on functional diversity and its different components (richness, divergence and evenness; (Carmona, de Bello, Mason, & Lepš, 2016; Mason, Mouillot, Lee, & Wilson, 2005)⁠ remains poorly understood (Esquivel-Muelbert et al., 2017; 2018; Poorter et al., 2015; Sakschewski et al., 2016) and still holds many knowledge gaps (Aguirre-Gutiérrez et al., 2019)⁠.

Vegetation models have been widely used to explore the fate of Amazon forest carbon sink under unprecedented climatic conditions such as reduced precipitation, providing substantial contribution to our current knowledge of the Amazon forest susceptibility (Cox et al., 2004; Galbraith et al., 2010; Huntingford et al., 2013; Lapola, Oyama, & Nobre, 2009; Rammig et al., 2010; Sitch et al., 2008)⁠. Although most of these models tend to project a drastic loss in carbon stock (P M Cox, Betts, Jones, Spall, & Totterdell, 2000; Peter M. Cox et al., 2004; Koch, Hubau, & Lewis, 2021⁠)⁠, in line with a replacement of the predominant vegetation by a drier-affiliated one in large portions of Amazon forest (Hutyra et al., 2005; Lapola, Oyama, & Nobre, 2009; Salazar, Nobre, & Oyama, 2007), some of the results are contradictory and often diverge between different models (Huntingford et al., 2013; Powell et al., 2013; Rammig et al., 2010). One of the reasons for model divergence may rely on the way that the diversity of vegetation is represented in most of these models, i.e., they commonly represent vegetation, based on a very small, discrete, and *a priori* defined set of plant types (PFTs), in which the parameters that represent functional traits responsible for ecophysiological process and the connection with environment (i.e., the responses and effects) are fixed in space and time for each PFT (Reu et al., 2014; Scheiter et al., 2013; Verheijen et al., 2015)⁠. This simplification of vegetation diversity seems to limit the ability of current DGVM to project with accuracy the impacts of environmental changes in terrestrial ecosystems (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Sakschewski et al., 2016; Verheijen et al., 2015). It occurs since the representation of diversity of functional identities and responses that could perform differently in a changing environment and deal better with the new conditions are very limited by the low number of PFTs (Fyllas et al., 2014; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016))⁠. Hence, the community functional reorganization, which is an important process that can confer resilience (Aguirre-Gutiérrez et al., 2019; Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), is very restricted or sometimes even not at all captured when applying a fixed plant functional type modeling approach (Sakschewski et al., 2016; Verheijen et al., 2015)⁠.

Hence, in an attempt to overcome these limitations regarding the underrepresentation of functional diversity by using PFTs , so-called trait-based vegetation models have been developed (e.g., Fyllas et al., 2014; Joshi et al., 2020; Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Sakschewski et al., 2015; Scheiter, Langan, & Higgins, 2013)⁠. This alternative modeling approach represents plant types in a less discrete manner by replacing the fixed-value parameters representing the 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), thus providing the opportunity of exploring a multiplicity of functional ecology-related questions that go beyond the commonly analyzed biogeochemical variables (Sakschewski et al., 2016; Darela-Filho et al., in prep.)⁠. For example, this opens up the avenue for exploring the role of different components of functional diversity (richness, divergence and evenness), as well as, the identification and prediction of processes that determine community assemblage and structure (Mouillot et al., 2013) and how this affects the resilience of the ecosystem against environmental changes (Mason, Mouillot, Lee, & Wilson, 2005; Song, Wang, Li, & Zhou, 2014).

Despite of the promising potential proposed for some of the trait-based approaches designed to explore these types of questions, so far many of these eco-evolutionary aspects highlighted in the scientific literature remain under-explored by the modeling community (but see: Hofhansl, Chacón‐Madrigal, Brännström, Dieckmann, & Franklin, 2021⁠). For example, few studies using trait-based models have explored how environmental changes affect functional diversity and each of its different components. Hence, in spite of the proposed mechanistic linkage between functional diversity and ecosystem functioning (Carmona, de Bello, Mason, & Lepš, 2016; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013)⁠, the ability of trait-based models to effectively capture (and improve) associated plant functional response to environmental changes, via representation of ecological processes, such as net primary productivity (NPP) and carbon storage (that are commonly represented in standard vegetation models) is yet to be assessed.

Here, we present a novel trait-based approach, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model. First, we evaluate CAETÊ’s performance in representing vegetation carbon storage and NPP for the Amazon basin region (Fig. SI.1). In order to assess if the inclusion of trait variation in fact improves the representation of these biogeochemical variables we compared two approaches of CAETÊ: one representing vegetation through a small number of PFTs (i.e., low functional diversity; hereafter PFTA) and the other one representing vegetation using variant functional traits (i.e., high functional diversity; hereafter TBA). Six traits were defined to be fixed (PFTA) or variant (TBA): carbon allocation and residence time in three plant compartments (leaves, aboveground woody tissues and fine roots). We further applied these two modeling approaches in a scenario of reduced precipitation, resulting in associated moisture deficits projected for the Amazon region, with the intent to evaluate (i) how moisture stress affects functional diversity components, (i.e., richness, evenness and divergence); and (ii) how associated shifts in functional community composition affect Amazon forest carbon stocks, by investigating the following hypothesis:

(H1) We expect that (in comparison with the standard PFT approach) the proposed trait-based modeling approach with variable trait combinations should result in the functional reorganization of the community under applied scenario of reduced precipitation((Walker, Kinzig, & Langridge, 1999; Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999)⁠, resulting in a higher capacity to maintain carbon vegetation stocks, in line with a more resilient ecosystem (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019).

(H2) A functional reorganization of plant communities in response to climate change (especially in the TBA) should prioritize strategies with higher investment in plant tissues that increase the acquisition of the most limited resource (i.e., a higher allocation to fine-roots to increase water uptake in the reduced precipitation scenario). This prioritization of strategies relies on the optimal partitioning theory (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972)⁠ due to environmental filtering of a small subset of functional trait combinations more suitable to cope with drought under the reduced precipitation scenario.

(H3) A selection towards more restrict range of functional traits values should lead to communities with lower functional richness (Cornwell et al., 2006; Funk et al., 2017; Kleidon, Adams, Pavlick, & Reu, 2009; Perronne & Gaba, 2017) and decreased evenness (via less regularly distributed density of traits values), thus favoring strategies in the communities with specialized functional traits and yielding an increase in divergence (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011)⁠. Together, the decrease in evenness and increase in divergence is supposed to lead to lower utilization of the functional space (De La Riva et al., 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011)⁠ and thus resulting in low resilience.

**Material and Methods**

*The CAETÊ model: an overview*

Here we present an overview of the CAETÊ, and an in-depth description of the model (including all the ecophysiological processes equations and input data) can be found in Supporting Information SI.1. As a trait-based model, CAETÊ is designed to capture the variability of plant functional traits and assess the range of functional diversity found in plant communities. As such, vegetation is represented by a set of functional strategies (hereafter called plant life strategies, PLS), each of which refers to a unique combination of functional traits values. that 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 (Fig. 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, thus representing 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 (for more details see Supporting Information SI.1.1.a.). The combination of all sampled values generates a large number (>105) of combinations within the functional space. Similar to 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 Supporting Information SI.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 in the model acts such that each PLS within the trait space performs differently under the same environmental conditions such as 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 in the simulation, it is expected that some PLSs will present different performances and abundances, such that some strategies will survive while others will be excluded of the spatial grain in the simulation (and cannot be reestablished).

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 so-called “Darwinian demons” (i.e., optimal but rather unrealistic strategies that maximize all the functions that contribute to plant fitness and thus increase an individual’s survival; 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 ecophysiological performance of a given PLSs 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 by the biomass-ratio hypothesis (i.e., increasing with plant biomass; Grime, 1998; see Supporting Information SI.1.1.b.). The ecophysiological processes linked to each functional trait, its trade-offs, and associated formulations are summarized in Table SI.1 and described in Information SI.1.10.

*Simulations setup*

In this study designed for the Amazon basin, we employed 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). An initial equilibrium spinup simulation is carried out by the calculation of carbon stocks in equilibrium in different plant compartments according to the C turnover of each functional identity and an estimate of local NPP. (see Supporting Information SI.1.1.c.)

Two versions of the model considering two different approaches were employed in this study: one, similar to the majority of currently applied vegetation models, using the PFTA [with a low functional diversity initialization: 3 PFTs (Table SI.2)], and the other, TBA, using a varying trait-based approach [with a high functional diversity initialization: 3000 PLSs (Table S.I.3)]. 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 approaches.

We employed six functional traits that are variable between PFTs/PLSs. Since the analysis presented here is focused on the assessment of vegetation carbon storage three of them regard the percentage of the carbon distributed to different plant tissues [i.e. carbon allocation to leaves, roots and aboveground woody biomass (hereafter ABGW)] and the other three traits represent carbon residence time (i.e., how long the carbon remains in living plant tissues) in respective plant tissue. Together, these functional traits ultimately define the amount of carbon in each plant tissue of a PLS or PFT at each time step, and are of primary importance for determining absorption and storage of carbon in the study system (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 encompassing the majority of PFTs previously used in standard vegetation models. The parameters that represent the functional traits used for this study were *a priori* defined following values already used in previous other vegetation models (Table SI.2). In the trait-based model approach, the initial range of values for each of the variable traits (which are used to create the hypervolume) are indicated in Table SI.3. CAETÊ works at a spatial resolution of 0.5º x 0.5º and is coded mainly in Fortran 90 with some modules written in Python.

*CAETÊ performance evaluation*

A first simulation run was designed to evaluate and compare the performance of the two approaches (PFTA and TBA) in representing the spatial distribution of vegetation carbon storage and NPP in the Amazon region. For this we compared our model results with reference data obtained from literature and databases through linear regression and by computing the absolute difference between values simulated by CAETÊ and those reference ones for each grid cell. For carbon storage we used data from Baccini et al. (2012) and Saatchi et al. (2011), and for NPP we used data from the MODIS (Moderate resolution imaging spectroradiometer) NPP Project (MOD17A3; Running & Zhao, 2021).

For carbon storage only the aboveground carbon was considered (leaves and aboveground woody tissues) since Baccini’s data comprises this vegetation portion and Saatchi’s data include estimates of belowground biomass through allometric equations. Besides, the reference data accounts for living biomass instead of only carbon content (as simulated by CAETÊ). Therefore, we considered that 47.5% of living biomass depict carbon content (Thomas & Martin, 2012 ).

Furthermore, we also compared CAETÊ results regarding carbon storage and NPP with *in situ* measurements available from the literature (Table SI.4) throughout the study area (Fig. SI.1). The comparison was made using linear regression. For coordinates where more than one measurement was available a mean value was considered. When the data corresponded to living biomass, only 47.5% of the value was considered (Thomas & Martin, 2012).

*Representation of functional diversity and composition*

Here we focused on a large-scale analysis of functional diversity across the Amazon basin, such that the trait distribution used to evaluate functional diversity should correspond to the distribution of the mean trait values obtained for each one of all the grid cells considered; hence, the trait variation within a grid cell is not considered. The mean trait values are estimated according to the relative abundances of PFTs/PLSs (see Supporting Information S.I.1.1.b.) using the Community Weighted Mean (CWM) metric (Díaz et al., 2007; Grime, 1998)⁠.

Functional diversity and composition is regarded here both from the perspective of its single-trait components (*i.e.,* each functional trait separately and independent of others) as well as its multi-trait component (*i.e.,* the combination of traits). Both the single-trait and multi-trait allowed us to asses how the community occupy the functional space and how it is functionally organized by computing its composition (occurrence and abundance of trait values), the relative dominance between trait values and the functional diversity components.

For the single trait analysis we constructed distribution curves of the functional traits occurrence following the methods proposed by Carmona et al. (2016). In this method, the full range of trait values is considered as the total functional trait space, and the occurrence and abundance of the trait values express the occupancy of this space as functional niches calculated through probability density distributions, the so-called TPDs (trait probability distributions). From trait distributions we assessed the three different functional diversity components following the definitions by Carmona et al.: (i) functional richness: amount of functional space occupied by the community, *i.e*, the total range of trait values for a specific functional trait considering all organisms (PFTs/PLSs in our case); (ii) functional evenness: the regularity of 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 PFTs/PLSs’ trait values are distributed towards the extremes of their functional trait space.

For a multi-trait functional diversity analysis, we used the hypervolume metric proposed by Blonder et al. 2014, which combines the distribution of *n* trait values to create a multidimensional functional space and calculates functional diversity components metrics from it (Barros et al., 2016; Blonder et al., 2018). Within such a hypervolume,⁠ functional richness can be interpreted as amount of volume that is occupied by the community relative to the potentially available functional space based on the frequency of trait values that composes this community. The distribution of trait values around the centroid (i.e., the variation around the mean value), can be used to assess the functional composition of the system (Barros et al., 2016). Following the recommendation by Barros et al. (2016), we performed a principal component analysis (PCA) with a centered and scaled method before creating the hypervolumes (for more details see Supporting Information SI.3). Using the factor scores on the chosen principal components (indicated in Supporting Information SI.3) we were able to meet the statistical assumptions for constructing the hypervolume (Blonder et al., 2014)⁠.

*Decreased precipitation experiment*

In this modeling experiment we applied a 50% precipitation reduction scenario for the study area. The reduction in precipitation was homogeneous, *i.e.*, it was applied for the whole period of the study and for all the grid cells equally. Since we are well aware that the frequency of a drought is not homogeneous through time or along environmental gradients across the basin, we did not intend to make reliable predictions of drought for the region. Instead, we used this 50% precipitation reduction scenario to test our three proposed hypothesis and as proof of concept by showing: (i) that the functional diversity of an ecosystem is tightly related to ecosystem processes and functioning, playing a vital role in its responses to environmental changes, and (ii) the potential of trait-based models for exploring the effects of environmental changes on functional diversity (taking into account its different facets) and its compound effect on ecosystem functioning.

To test our hypothesis H1, we first compared the degree of change in carbon stock between the two employed modeling approaches. Then, to understand the role of functional diversity in this change we assessed the if the the plant communities were significantly modified, that is, functionally reorganized, by the climatic forcing scenario. For this, we computed dissimilarities index (degree of overlap) between the TPDs before and after reduced precipitation application for each of the modeling approaches. This index varies from 0 (*i.e*., completely functionally similar) to 1 (*i.e*., completely functionally different) following Carmona, de Bello, Mason, & Lepš (2016). We also evaluated the changes in hypervolume with precipitation reduction computing the degree of overlap through Jaccard similarity index that ranges from 0 (completely dissimilar) to 1 (completely similar). Complementarily,

we compared the degree of centroid displacement between TBA and PFTA, what indicates how much the mean values of the communities were dislocated from their pre-disturbance location within the hypervolume. It was done by calculating the distance between the centroids before and after the disturbance application.

The second defined hypothesis concerns the changes on functional composition imposed by reduced precipitation. For the single-trait framework we analyzed the changes on curves generated by the TPDs, *i.e.,* we evaluated the change on the traits abundance of throughout the functional space showing, for example, the exclusion f trait values and/or increase in the occurrence of trait values that was rare before the disturbance.

The test of the third hypothesis was made by accounting for the percentage change of the three facets of functional diversity (i.e., species richness, evenness, and divergence) after the application of reduced precipitation in the case of single-trait analysis. For the multi-trait analysis we compared the change on volume sizes, that represent shift in the community richness. For that, we constructed four hypervolumes using the factor scores of the previous performed PCA: one for each model approach (TBA/PFTA) and climatic scenario (regular climate/reduced precipitation); we further compared the two hypervolumes of each model approach.

**Results**

*Reduced precipitation impacts on carbon storage: the role of trait variability*

The 50% reduction of precipitation caused a widespread depletion of carbon stocks along the basin, including grid cells that presented a total carbon loss for both employed model approaches (Fig. 3a and b). Nevertheless, the spatial pattern of carbon loss differed between them: TBA was able to maintain carbon stocks in some areas where in PFTA carbon stocks were completely lost, that is, none PFT survived in those grid cells. This was more evident in central Amazon and in naturally drier areas, such as the transition between the Amazon forest and the savannah (*cerrado*) in the southeast region. It is also noteworthy that the loss of carbon in TBA, unlike in PFTA, was more gradual, *i.e.*, it presented a smoother gradient between a grid cell value and its neighboring cells, and also across different basin regions. However, as an unexpected and contradictory result, in specific grid cells where both modeling approaches were able to maintain at least a minimum carbon stock, PFTA presented a higher value of carbon storage than TBA (Fig. 3a and b).

Specific plant compartments have shown different patterns of changes when comparing the two approaches (Fig. 3c and 3d for fine roots, Fig. SI.4a and b for leaves and Fig. SI.4c and d for ABGW). None of the compartments has shown an increase in carbon stock with precipitation reduction, except for the fine roots compartment in TBA (blue areas in Fig. 3d). It was more evident in the transitions from humid and evergreen forest to the Brazilian savannahs (*cerrado*) and also in the northwest of the basin (naturally drier sites). The increased investment in fine roots also indicated change in carbon partitioning (root:shoot relation) towards higher belowground investment in TBA but lower belowground investment in PFTA: we found an average increase of 74.74% on this relation for TBA while for PFTA an average decrease of 7.73% was observed.

*Effects of reduced precipitation on functional composition*

We found a high value of dissimilarity index (close to 1; Table 1) for the six plant functional traits for both PFTA and TBA together with changes in the traits probability density distributions (Fig. 4). A clear change in the pattern of the TPDs, and as a consequence on composition, was observed: a a reduction in hyperdominance (decrease of the peaks of the curves) of a previously restricted range of values, and density increase of other trait values that were previously rare (very low density), or absent (Fig. 4). Also, with the applied change in precipitation, the hypervolumes for TBA and PFTA showed a pronounced modification (Fig. 5 and SI.5; see Movie SI.1 for a 3D animated representation): 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 between the hypervolumes. Besides, the distance between the centroids of the two hypervolumes after imposing a climatic change indicated a change in the mean values and in the composition: the centroid distance for the TBA was 5.25 and 0.937 for the PFTA.

Although the two approaches have shown considerable changes in their functional composition, the degree of these changes was different between them: when considering traits separately, the PFTA showed a trimodal distribution, with three clear and discrete peaks along the trait space, but without alteration in the range of values (Fig. 4d-f and 4j-l). 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 (Fig. 4a-c and 4g-i). In general, TBA showed an increase in density towards higher values of carbon allocation in fine roots and towards lower values of carbon allocation in leaves and, especially, in ABGW (Fig. 4a-c), and an increase in residence time for leaves and for fine roots but a decrease for ABGW (Fig. 4g-i). The same spatial pattern distribution along functional space observed for single-traits arised when considering all traits together through the hypervolumes: for the PFTA it was possible to observe three clear data grouping under drought (Fig. 5a), and a much less discretized data distribution from the TBA (Fig. 5b). The distance between the centroids also shows that the mean values (composition) were modified in a higher magnitude for the TBA when compared to the PFTA approach with the applied reduced precipitation.

*Reduced precipitation impacts on functional diversity facets*

The alterations in the density distribution of curves drove changes in the three facets of functional diversity, however for all of them, the change was in a much lower degree for PFTA when compared to TBA. We found an increase in functional richness for all traits in both approaches, except for residence time in ABGW for the PFTA (Fig. 6a). For all the traits in the TBA, we observed an increase superior to 100% for functional evenness, while in the PFTA, the change was the opposite: traits showed a decrease in this functional diversity component, except for allocation and residence time in AGBW (Fig. 6b). Concerning divergence, TBA showed an increase of more than 200% for leaf allocation trait, while the other TBA traits displayed a reduction of this variable (Fig. 6c). The PFTA presented an increase in divergence for all functional traits, with the exception of leaf allocation and residence time in ABGW (Fig. 6c). In the multi-trait perspective we observed an increase in richness, both for TBA and PFTA, due to the increase of volume occupied by the communities within the functional space (Fig. 5 and SI.5). The former presented an increase in the size of the volume in a higher degree than the latter: under natural climatic conditions the size of the volume that the data occupied was equal to 1.71 and 0.007 for TBA and PFTA, respectively; while under reduced precipitation we found a volume size of 47.84 for TBA and 0.75 for PFTA.

*CAETÊ model performance evaluation*

We found that both employed modeling approaches, to some extent, show disparities (under or overestimation) for carbon stock and NPP values when compared to the reference data; however, TBA presented a better agreement with reference data for all the analyzed variables.

In terms of spatial patterns in carbon stock, both approaches overestimate the values at the basin edges and PFTA also tends to a general overestimation throughout Amazon basin with emphasis on the central region (Fig. 2). On the other hand, TBA tends to underestimate mean carbon values in some regions, for example in the east and southwest of the basin. Even so, TBA presents more areas with no differences between simulated and reference values (white cells in Fig. 2b and e) as well as higher number of points closer to the 1:1 line when compared to PFTA (Fig. 2c and f), matching the observed values reasonably well. Also, within the studied region, this approach simulated a total aboveground carbon stock much closer to references than PFTA: 80.2 and 71.7 PgC for Baccini et al. (2012) and Saatchi et al. (2011), respectively; while PFTA simulated 127.9 PgC and TBA 86.0 PgC.

In regard to NPP comparison with remote sensing NPP estimation (MODIS; Running & Zhao, 2021), TBA reveals reasonably well ability is able to capture the broad spatial patterns (Fig. SI.2b), despite an underestimation at Andean region and a small overestimation in the northwest/central basin region. On the other hand, PFTA presents a widespread and prominent overestimation for this variable (Fig. SI.2a), except for the underestimation at the Andean region. The higher agreement of TBA with MODIS data when compared to PFTA can also be seen in Figure SI.3c, which shows a grid-by-grid cell performance comparison between CAETÊ and MODIS. The CAETÊ model simulated a total annual NPP of 122.28 PgCyr⁻¹ (PFTA) and of 76.05 PgCyr⁻¹ (TBA) for the studied region. Estimates based on MODIS arrived at a value of 74.61 PgCyr⁻¹ (Running & Zhao, 2021). Thus, the total NPP value simulated by CAETÊ in its trait-based version (TBA) is much closer to the value estimated by MODIS.

Finally, the direct comparisons between simulated values and *in situ* measurements of aboveground carbon storage, total carbon storage and NPP showed similar patterns to previous comparisons, i.e, overestimation of all variables by PFTA and underestimation by TBA (Fig. SI.3).

**Discussion**

Our results showed that the applied moisture stress scenario induced to a loss of carbon throughout the study region in both modeling approaches, however we observed a more subtle or smoother carbon losses in the TBA, which also showed areas where carbon stock was maintained but where none PFT were able to survive in PFTA. Carbon stocks were reduced in all the plant compartments, except for fine roots in TBA, that presented an increase of investment in this tissue. Both modeling approaches showed changes in the density distribution curves of traits and in the size of the volume occupied within functional space. As a consequence, the three facets of functional diversity were modified under reduced precipitation, however the magnitude of the change was much higher in TBA. We also found that TBA presented better performance in representing carbon stocks and NPP against estimations/observations in comparison to PFTA.

*Carbon stocks under reduced precipitation: does the modeling approach matter?*

We found that in accordance with our first hypothesis, in fact, the inclusion of trait variability in vegetation models matters for evaluating impacts of environmental change in ecosystems: the trait-based modeling approach presented lower sensibility in terms of carbon storage loss with precipitation reduction when compared to the modeling approach based on PFTs (Fig. 3). In line with our findings, it is widely accepted that a more diverse (both taxonomically and functionally speaking) ecosystem tends to be less impacted by environmental changes (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019). This can be attributed to the fact that higher variability of traits (and plant strategies) also provides higher diversity of responses under new environmental conditions (Mori, Furukawa, & Sasaki, 2013; Yachi & Loreau, 1999)⁠. In that sense, our results contributes to reinforce the “insurance hypothesis” which postulates that the diversity of responses insures ecosystem functioning by providing a buffer effect against environmental fluctuations (Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999). In a functional perspective, such an effect is expected through a compensation process called as “functional density compensation” when the composition (that is, the occurrence or abundance of trait values) of a community adjusts to the new conditions enabling types of plant that previously exerted a less relevant functional role (i.e. low density) to increase their dominance and vice-versa. It is a reflection of a functional reorganization of the community that compensates losses or decrease in dominance of strategies, insuring ecosystem functioning (Gonzalez & Loreau, 2009; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016)⁠. 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; Morera-Beita et al., 2019; Mouillot et al., 2013; van der Sande et al., 2017).⁠

Such a functional density compensation followed by functional reorganization after a precipitation reduction was well captured in our modeling results: similarity/dissimilarity indexes (for the single and the multi-trait perspectives) together with the centroids displacements showed that the functional structure of the plant communities was significantly modified by the climatic forcing scenario. Although both approaches have shown significant functional restructuring, as hypothesized (H1), the ability to functionally reorganize was much higher in the model with a more diverse community (TBA), what conferred more resilience to the community to deal with the new environmental conditions.

*Functional composition and the selection of plant life strategies*

Here we found that the TBA higher capacity to functionally reorganize enabled a paramount change in the community composition of this modeling approach that corroborates with our H2: a prioritization of plant strategies with higher investment in fine roots through the increase in the abundance of traits with higher values of allocation and residence time for fine roots (Fig. 4c and e). The higher investment in roots was to the detriment of investment in leaves (Fig. 4a and g) and ABGW (Fig. 4b and h) what reflected in a change on carbon partitioning for TBA: a bigger root:shoot ratio when compared to the regular climate condition. This change increased the uptake of water, what allowed the community of TBA to better deal with the imposed moisture stress and maintain carbon stocks or reduce the degree of biomass loss. These results corroborate with the well known effect of climatic change, such as drought, in inducing 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)⁠. On the other hand, given the limited trait variability, PFTA did not show this plasticity in the allocation of carbon to different plant tissues, causing a depletion of the basic plant metabolism maintenance, a mechanism also known as carbon starvation (McDowell & Sevanto, 2010), that increased mortality rates and avoided the PFTs to establish in some grid cells, turning the ecosystem, in general, more vulnerable (Fig. 3a).

However, because of the changes in root:shoot ratio in TBA, we also observed grid cells in which the amount of carbon stock in the PFTA was higher than in the TBA with the applied reduced precipitation (Fig. 3a and b). It highlights that understanding such shifts in carbon partitioning in response to climate change is of primary relevance for the future predictions of Amazon carbon stocks (Doughty et al., 2015; Friedlingstein et al., 2006; Koch et al., 2021)⁠, and is especially reasonable if the carbon is allocated towards pools with shorter turnover times, such as fine roots or even root exudates (Jiang et al., 2020)⁠, that in comparison with woody tissues contribute to a lesser extent to total carbon storage (Chave et al., 2009; De Kauwe et al., 2014; Kannenberg et al., 2019; Luo, 2003)⁠. Our modeling exercise was able to capture this process: the reduced precipitation input triggered an increase in investment in fine roots in the TBA that provided greater resistance to drought, preventing the total loss of carbon in several grid-cells, but also led to a lower carbon storage in other tissues, mainly on ABGW, what resulted in 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 assessed by currently applied vegetation models, it may result in flawed interpretations about the response of tropical forests to climate change ( e.g., Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016). Our results highlight that the approach used to represent the impacts of environmental change in ecosystem models does indeed matter, since we found that the use of a small set of PFTs with fixed parameters can overestimate the impacts of environmental changes and hinder the identification of processes such as the change in functional community structure.

*Environmental changes modify functional diversity components*

It is expected that changes in environmental conditions may alter functional diversity components since disturbances affect how the community occupy the functional trait space through changes in abundance, what in its turn affects ecosystem functioning (Boersma et al., 2016; Carmona, de Bello, Mason, & Lepš, 2019, Enquist et al., 2017⁠)*⁠.* However, so far, few studies have explored how environmental controls affect trait variability within the functional space and other components of trait variation such as the different functional diversity facets (but see Hofhansl, Chacón‐Madrigal, Brännström, Dieckmann, & Franklin, 2021)⁠ and how it could impact communities sensibility to environmental changes.

In accordance, our results showed that the reduced precipitation caused a modification in the way that traits occupy the functional space (Fig. 4 and Fig. 5) and in the functional diversity facets (Fig. 6). However the two modeling approaches here employed showed distinct results both regarding the direction (except for richness) and magnitude of changes on functional diversity what conferred important consequences for their sensibility to the applied disturbance. The distinct results, mainly regarding the magnitude of change, derived from the higher ability of TBA to functionally reorganize when compared to the TBA. For example, reduced precipitation led to an expressive wider range of traits values in functional space in the TBA, both in a single and in a multi-trait perspective, enabling the occurrence of trait values that was not present present before the disturbance or increasing their occurrence (Fig. 4 and Fig. 5), that is, increase in richness (Fig. 6a). On the other hand, PFTA presented a restricted probability of the occurrence of new trait values, showing trimodal curves with lower precipitation (Fig. 4), three discrete groups in the hypervolume (Fig. 5) and a lower degree in richness increase (Fig 6a).

These results are not in accordance in our third hypothesis, in which we expected a lower functional richness due to a stronger environmental filtering imposed by the reduced water availability (Boersma et al., 2016;⁠Cornwell et al., 2006; Funk et al., 2017; Perronne & Gaba, 2017). But our findings might be explained by the decisive role that the decrease in hyperdominance exerted after the applied disturbance, since it allowed new combinations of traits to establish or to increase their occurrence (Walker, Kinzig, & Langridge, 1999)⁠. These results provide further evidence that, in some cases, functional richness can increase in disturbance scenarios if the environmental change affects mainly the dominant plant strategies (Boersma et al., 2016; Funk et al., 2017; Mouillot et al., 2013).⁠

Also contrary to H3, evenness exhibited an increase for all considered traits for the TBA (Fig. 6b). On the other hand, the PFTA showed a decrease in this functional diversity component for the majority of traits (Fig. 6b). 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 around three peaks of the density distribution function and thus turning the distribution less even in the reduced precipitation scenario (Fig. 4d-f and j-l). 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, contrary to our expectations in H3, thus providing a lower sensibility to environmental changes, if it presents a sufficient variability in its trait values, as we observed for the TBA.

Since we expected a more restrict occurrence of trait values with the disturbance application, we assumed an increase in divergence (H3). It means that, to deal with the imposed environmental change, the community would be supported by the abundance increase of more specialist strategies in terms of trait values (Mouillot et al., 2013; Villéger, Miranda, Hernández, & Mouillot, 2010)⁠. However, contrary to our expectations we observed a general decrease in divergence in the TBA (Fig. 6c), caused by the expressive decrease in abundance of previous dominant trait values, which tended to concentrate at the extremes of functional spaces; as a consequence, other trait values that were not so abundant became significant after the disturbance. Based on an empirical evidence by analyzing a disturbance gradient, Mouillot et al. (2013) also found a decreasing divergence the greater the disturbance, which was attributed to a declining abundance of the specialist species that were the most impacted by the disturbance. In addition, this decrease in divergence can be an evidence that the frequency distribution of trait values in the functional niche space maximizes the total community variation in functional characters (Mason et al., 2005). In contrast, PFTA showed a general increase in divergence (Fig. 6c), which may be a product of the emergence of the three peaks in the trait probability distribution. For this approach an improvement in the occupation of functional space (low divergence) is impossible considering its very low diversity of trait values available, what confer higher sensibility to disturbances (Villéger et al., 2010).

*Trait variability inclusion and model performance*

Our results support the statements of trait-based models developers that the inclusion of trait variation in vegetation models in fact plays a key role in predicting vegetation carbon cycle for present and for future projections. We found that the TBA was not only able to represent NPP and carbon storage reasonably well when compared to references , but also showed higher agreement when contrasted to PFTA performance (Fig. 2, Fig. SI.2 and Fig. SI.3). Indeed, the improvement in accuracy in projected biogeochemical variables was already observed in other studies that added trait variability to existing modeling approaches (Fyllas et al., 2014; Sakschewski et al., 2015; L. M. Verheijen et al., 2013; Lieneke M. Verheijen et al., 2015). The trait variability inclusion confers a higher diversity of responses in communities to environmental filtering derived from climatic heterogeneity allowing a more realistic simulation of the community assembly (Keddy, 1992)⁠ and, as a consequence of the biogeochemical cycles (Sakschewski et al., 2015; Verheijen et al., 2013; Westoby et al., 2002)⁠.

However, both modeling approaches presented some mismatch when compared to the reference maps. For example, the PFTA showed a generalized overestimation of aboveground carbon storage and NPP (Fig. 2a and d and Fig. SI.2a and c). It is derived from the fact the PFTs (chosen by previous PFTs implemented in DGVMs) are already parameterized to present a high performance (or optimal trait combination) in the climatic envelope found in regions with predominance of tropical forests (Scheiter, Langan, & Higgins, 2013; L. M. Verheijen et al., 2013)⁠. It allows an elevated occurrence of PFTs with higher carbon storage, which is especially important in our simulations, since our upscaling from the community to the grid-cell is weighted by the biomass of PFTs/PLSs present in this cell.

Also, both approaches presented a tendency to overestimate carbon storage and NPP at the edges and at the central/northwest of Amazon basin (Fig. SI.2). These inconsistencies could be attenuated through the improvement of some caveats that the CAETÊ model presents. First, the overestimation of the biogeochemical variables at the basin edges can linked to the lack of representation of human land use or fire for determining vegetation distribution in the model (Houghton, Lawrence, Hackler, & Brown, 2001; Ometto et al., 2014; Saatchi, Houghton, Dos Santos Alvalá, Soares, & Yu, 2007)⁠. Another important caveat of this study is that the model does not yet present a plant hydraulics module, then we were not able to use variant traits that are directly connected to moisture stress impacts on essential plant hydraulics features, such as vulnerability to cavitation and embolism (Joshi et al., 2020; Papastefanou et al., 2020)⁠. This representation is crucial considering that several studies have claimed that the decrease in carbon storage due to moisture stress is not, necessarily, linked to a decrease in carbon availability (i.e., carbon starvation) 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 does not consider the effects of biotic interaction such as mechanistic competition and facilitation, what seems to play a vital role in determining community assembly and ecosystem functioning (Falster, Brännström, Westoby, & Dieckmann, 2017; Kunstler et al., 2016; Mori, Furukawa, & Sasaki, 2013)⁠. Beyond, nutrient cycling representation on vegetation models, mainly nitrogen and phosphorus, have been shown to be essential for a reliable representation of carbon storage along Amazon basin (Fleischer et al., 2019)⁠. In that sense, we strongly recommend that further studies using vegetation models, including CAETÊ, that aim to understand the impacts of moisture stress on Amazon forest carbon stock, should consider land use changes, plant hydraulics traits, biotic interactions and nutrient cycling.

Regarding functional diversity analysis, for this study, we considered the whole Amazon basin as a single ecological unit, which may lead to an oversimplification of diversity within the basin. To avoid this, we strongly recommend that future studies consider using the framework described in Carmona et al (2016) to integrate functional diversity across scales, in this case from grid cells to the whole Amazon basin. By employing this framework, it would be feasible to investigate functional diversity in different Amazon basin regions, and it could be used to advance further on the understanding of the connection between functional diversity and ecosystem functioning.

**Conclusions**

The need for a more reliable representation of functional diversity in vegetation models and, consequently, a higher confidence in its projections have led to the development of trait-based models. However, few studies so far have investigated in depth if the inclusion of trait variability in fact improves the representation of ecosystem properties such as NPP and carbon storage, an important refinement that could improve reliability of projections of terrestrial ecosystems under ongoing climate change. Furthermore, the potentiality of trait-based models to tackle functional ecology-relevant questions, such as the role of functional diversity, and its different components, in resilience against climate change, is yet to be explored more deeply.

In this modeling exercise, we compared, for the first time: (i) how the use of a PFT approach (PFTA) differs from a trait-based (TBA) approach in terms of current representation of carbon storage and NPP; (ii) the impacts of a reduced precipitation scenario on how these two approaches simulate carbon storage and functional diversity and (iii) how changes on functional diversity components due to lower water availability are connected to the carbon storage responses of the two modeling approaches. The use of a PFTA and a TBA in the same vegetation model provides a proof of concept on the significance of incorporating functional diversity in vegetation models. Our results evidenced, for example, that the inclusion of trait variability improve accuracy in representing biogeochemical variables and also show that trait-based models, such as CAETÊ, are important tools to investigate mechanisms and processes that link biodiversity (mainly functional diversity), ecosystem functioning and resilience. Consistent with expectations, we found that more diverse communities (trait-based approach) deal better with environmental changes since it provides a higher range of responses, which enables the community to functionally reorganize buffering, by maintaining or diminishing, the impacts of disturbances in ecosystem properties. On the other hand, because of its limited capacity to change community functional structure, the use of a small number of PFTs overestimates the impacts of environmental changes.

Moreover, the trait-based method here presented, emphasizes the importance of exploring the impacts of climate change in functional diversity and its connection with ecosystem functioning. In that sense, we unexpectedly found that a harsher environment can increase occupation of the functional space. It can be attributed to a reduction in hyperdominance and then to the creation of new functional ecological niches for new combinations of traits, or hitherto rare combinations, promoting an insurance of ecosystem properties and decreasing the ecosystem sensitivity to environmental changes. These results highlight that our trait-based model framework can be used to understand the still uncertain connection between diversity and ecosystem functioning, especially in what concerns about the role of diversity in resilience of ecosystems but also other ecological questions such as the community assembly rules and biogeographical patterns of functional diversity.

In conclusion, this study demonstrated that the CAETÊ framework for including trait diversity in vegetation model is feasible and can be used in future studies, being flexible enough to be applied in several climatic scenarios and using different variable functional traits, hence, constructing a robust foundation to advance our understanding of the impacts that climate change will pose on hyperdiverse tropical ecosystems, such as the Amazon forest.

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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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