**Higher functional diversity improves modeling of Amazon forest carbon storage**

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**Highlights**

* New trait-based model to explore functional diversity role on climate change impacts.
* Combinations of trait values in a hypervolume create unique plant life strategies.
* Trait variability improves representation of vegetation carbon storage and NPP.
* Trait variability reduces vulnerability due to community ability to functionally reorganize.
* Impacts on functional diversity components affect simulated carbon storage.

**Abstract**

The impacts of reduced precipitation on functional diversity and how its components (richness, evenness, divergence and composition) modulate the Amazon carbon sink remain elusive. We present a novel trait-based approach, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model to investigate the role of trait diversity for projecting carbon storage and net primary productivity (NPP) in current climatic conditions and the impacts on carbon storage under low precipitation, by using two approaches to represent functional diversity: (i) Plant Functional Type Approach (PFT-approach) including three PFTs, and (ii) a varying Trait-Based Approach (TB-approach) including 3000 plant life strategies (PLSs). Six traits were considered: carbon allocation and residence time in leaves, aboveground woody tissues and fine roots. Trait variability improved performance in representing NPP and carbon storage. Reduced precipitation caused a similar decrease in total carbon storage for PFT-approach and TB-approach (~60%) but carbon loss in PFT-approach was more sharpened and widespread within grid cells. This difference owes to the TB-approach's higher ability to functionally reorganize through changes in PLSs abundance and in functional diversity (increase in richness and evenness and decrease in divergence). Consequently, functional niches were created in TB-approach, enabling new/previously rare trait combinations to emerge from the available plant life strategies pool. Then, TB-approach selected strategies that invest more in fine roots which made the community less sensitive to limited water availability but led to a higher root:shoot ratio (increase of 74.74%) resulting in relatively lower carbon storage in some grid cells. The use of only three PFTs overestimated the impacts of reduced precipitation due to limited capacity to reorganize, and results from the PFT-approach should be interpreted with caution. Our findings suggest that functional diversity is primordial when evaluating ecosystems sensitivity to climate change and that including trait variability in models enables more realistic future projections, thus paving the way for better understanding biodiversity-ecosystem functioning relationship.

**Keywords:** trait-based modeling, climate change, carbon allocation, functional trait space, functional reorganization, trait variability

**1. Introduction**

For the 21st century, it is projected that the Amazon forest will experience more frequent and more extreme moisture stress (IPCC, 2021)⁠, which can induce biodiversity shifts, including changes in functional diversity (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018) and impact vegetation ability to store carbon (da Costa et al., 2010; Hubau et al., 2020)⁠. However, how these climatic changes will affect different components of functional diversity (composition, richness, evenness and divergence; Carmona et al., 2016; Mason et al., 2005) and the role it plays in determining forest carbon storage response remains poorly understood (Esquivel-Muelbert et al., 2017; 2018; Poorter et al., 2015; Sakschewski et al., 2016).

Functional diversity and its different components plays a vital role in determining ecosystems functioning and its responses to disturbances (Díaz & Cabido, 2001; Song et al., 2014; Cadotte, 2017). Ultimately, are the functional traits that compose the communities that respond to biotic and abiotic conditions and also determine ecosystem processes and properties such as carbon storage (Lavorel & Garnier, 2002; Funk et al., 2017; Violle et al., 2007). For example, it is widely accepted that more taxonomically and functionally diverse communities tend to be less impacted by environmental changes (Cadotte et al., 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019). It has its basis on the “insurance hypothesis”, which postulates that the fact that higher variability of traits (and plant strategies) also provides higher diversity of responses under new environmental conditions (Mori et al., 2013; Yachi & Loreau, 1999) insuring ecosystem functioning by providing a buffer effect against environmental fluctuations (Fauset et al., 2015; Lohbeck et al., 2016; Yachi & Loreau, 1999). Such a buffering effect is expected through the process of functional density compensation, when the functional composition of a community (*i.e.*, the occurrence or abundance of trait values) reorganize and adjusts to the new conditions, enabling types of plants that previously exerted a less relevant functional role (low density) to increase their dominance and vice versa (Mori et al., 2013).

Hence, environmental changes lead to changes in the abundance of plant strategies that compose the communities and, as a consequence, how they occupy the available functional trait space and determine the different functional diversity components (namely: richness, evenness, divergence; Boersma et al., 2016; Carmona et al., 2019; de Bello et al., 2021 Enquist et al., 2017⁠)*⁠.* For example, reduced precipitation can act like an environmental filtering by selecting a small subset of functional trait combinations that are more suitable to cope with moisture stress. In such a scenario, according to the optimal partitioning theory (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972)⁠, it is expected the selection of strategies that invest more carbon to fine roots to acquire the most limiting resource that is water, in this case. The selection toward a more restricted range of functional trait values can conduct the community to occupy a smaller region of functional trait space (Cornwell et al., 2006; Funk et al., 2017; Kleidon et al., 2009), thus changing all functional diversity components and impacting ecosystem functioning.

Vegetation models have been widely used to explore the fate of the Amazon forest carbon sink under unprecedented climatic conditions such as reduced precipitation (Cox et al., 2004; Galbraith et al., 2010; Huntingford et al., 2013; Lapola et al., 2009; Rammig et al., 2010; Sitch et al., 2008)⁠. Some of these models project a drastic loss in carbon stock (Cox et al., 2000, 2004; Koch et al., 2021⁠)⁠ and an abrupt replacement of the dominant humid tree cover with more arid-affiliated vegetation in large portions of Amazon forests (Hutyra et al., 2005; Salazar et al., 2007). One of the causes that may contribute to these severe projections is the way that models represent diversity of plants (Pavlick et al., 2013; Scheiter et al., 2013)⁠. Commonly, the models represent vegetation based on a very small and discrete set of PFTs[[1]](#footnote-1) and the parameters that represent plant functional traits are previously (*a priori)* defined (Prentice et al., 2007)⁠. Hence, the diversity of plant life strategies found in these ecosystems is very simplified and alternative trait combinations that could perform differently in a changing environment and better handle the new conditions is very limited by the low number of PFTs (Fyllas et al., 2014; Mori et al., 2013; Sakschewski et al., 2016)⁠. Then, important mechanisms that can confer resilience, such as functional reorganization (Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), are restricted or sometimes even not captured at all. It may be hampering vegetation models to accurately project the impacts of environmental changes in terrestrial ecosystems (Pavlick et al., 2013; Sakschewski et al., 2016; Verheijen et al., 2015), mainly by overestimating these impacts.

Hence, in an attempt to overcome these limitations of underrepresenting functional diversity with PFTs, so-called trait-based vegetation models have been developed (*e.g.*, Fyllas et al., 2014; Joshi et al., 2020; Pavlick et al., 2013; Sakschewski et al., 2015; Scheiter et al., 2013)⁠. This alternative modelling approach represents plant types in a less discrete manner by replacing the fixed-value parameters that describe the small number of PFTs, with variable ones (Pavlicket al., 2013⁠; Reu et al., 2014; Webb et al., 2010; Wullschleger et al., 2014), ultimately incurring into a considerably higher number of trait combinations (one to three orders of magnitude more). It provides the opportunity to explore multiple functional ecology-related questions that go beyond commonly analyzed biogeochemical variables (Sakschewski et al., 2016; Darela-Filho et al., in prep.)⁠. For example, this approach opens up the avenue for exploring the role of different components of functional diversity, as well as identifying and predicting processes that determine community assemblage and structure, and how this affects the resilience of the ecosystem to environmental changes (Mason et al., 2005; Mouillot et al., 2013; Song et al., 2014).

Despite the promising potential of some of the trait-based approaches designed to explore these types of questions, thus far, many of these functional ecological aspects highlighted in the scientific literature remain underexplored by the modeling community (but see: Hofhansl et al., 2021⁠). For example, few studies using trait-based models have explored how environmental changes affect functional diversity and each of its different components. Hence, despite the proposed mechanistic linkage between functional diversity and ecosystem functioning (Mason et al., 2005; Mouillot et al., 2013)⁠, the ability of trait-based models to effectively capture (and improve) associated plant functional responses to environmental changes has yet to be tested.

To this end, we present a new trait-based model, the so-called CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model. To assess the importance of trait variability inclusion in vegetation models we compare two approaches of CAETÊ: PFT-approach[[2]](#footnote-2) and TB-approach[[3]](#footnote-3) Six traits are defined as either fixed (PFT-approach) or variant (TB-approach): carbon allocation and residence time in three plant compartments (leaves, ABGW[[4]](#footnote-4) and fine roots). In order to evaluate whether traits diversity in fact improves the representation of these biogeochemical variables we compared the modelling approaches performance in representing vegetation carbon storage and NPP for the Amazon basin region (Fig. SM.1). We further applied these two modeling approaches in a scenario of reduced precipitation in the same study area, which results in associated moisture deficits projected for the Amazon region, with the intent to evaluate (i) how moisture stress affects functional composition and functional diversity components (namely, richness, evenness and divergence) and (ii) how these shifts in functional diversity affect Amazon forest carbon stocks. We investigate the following hypothesis:

(H1) Compared to the standard PFT-approach, the TB-approach will result in the functional reorganization of the community under an applied scenario of reduced precipitation⁠, leading to a higher capacity to maintain carbon vegetation stocks, in line with a less sensitive ecosystem. On the other hand, as in the PFT-approach the functional reorganization to deal with the new conditions is restricted, we expect that in some grid cells PFTs will not be able to establish.

(H2) The functional reorganization of plant communities in response to reduced precipitation in the TB-approach will prioritize strategies with higher investment in plant tissues that increase acquisition of the most limiting resource, that is a higher allocation to fine roots to increase water uptake in the reduced precipitation scenario.

(H3) The prioritization of strategies will lead to the the selection toward a more restricted range of functional trait values in response to reduced precipitation reducing functional richness (Cornwell et al., 2006; Funk et al., 2017; Kleidon et al., 2009) and decreasing evenness (via a less regularly distributed density of trait values), thus favoring strategies in communities with specialized functional traits and producing an increase in divergence (Mouillot et al., 2013; 2011)⁠. Together, the decrease in evenness and increase in divergence are supposed to lead to lower utilization of the functional trait space (De La Riva et al., 2017; Hillebrand et al., 2008; Mouillot et al., 2011)⁠

**2. Material and Methods**

*2.1. The CAETÊ model: an overview*

Here we present an overview of the CAETÊ model, and for an in-depth description of the model and associated equations see Supplementary Material SM.1. In its trait-based approach, CAETÊ is designed to capture the variability of plant functional traits and assess the functional diversity found in plant communities. As such, vegetation is represented by a set of functional strategies (hereafter called plant life strategies, PLSs). The underlying premise for creating 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 et al., 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 values of functional traits that compose these combinations are semi randomly sampled from the complete range of values (for more detail, see SM.1.1.a.). The volume that all possible combinations occupy together can be seen as a potential functional space with a large number (>105) of combinations. Similar to other trait-based models (*e.g*., Pavlick et al., 2013; Reu et al., 2011), CAETÊ assumes that sampling an appropriate number of PLSs from the potential functional space (see sensitivity test in SM.2.), combined with an environmental filtering mechanism, allows the model to produce reasonable biogeochemical and functional diversity patterns.

The functional trait values assigned to each combination describe its ecophysiological behavior and its relationship with the environment. For example, it determines the differential capture of carbon, water and light through the differential combination of functional traits. Therefore, the functional traits of a plant strategy ultimately determine its performance in a grid cell (abundance and presence/absence). The differential survival and abundance between PLSs is also possible because each functional trait is related to at least one trade-off (cost-benefit relationship; Pavlick et al., 2013; Reu et al., 2014)⁠ which leads to a different relative performance. Additionally, the trade-offs prevent the model from creating so-called “Darwinian demons”, in other words, optimal but rather unrealistic strategies that maximize all the functions that contribute to plant fitness and survival (Scheiter et al., 2013)⁠. The ecophysiological processes linked to each functional trait, its trade-offs, and associated formulations are summarized in Table SM.1 and described in Supplementary Material SM.1.10.

The relative abundance () of a plant life strategy is the fraction of the grid cell that it occupies based on the carbon stock contribution of this strategy () in relation to the sum of carbon stock in this grid cell () for the number of present PLSs ().

|  |  |  |
| --- | --- | --- |
|  |  | (1) |
|  |  | (2) |

This procedure has support on the biomass-ratio hypothesis (Grime, 1998) that predicts that the immediate effects of a species is proportional to its relative contribution to the total biomass of the community. Then, from the relative abundances it is possible to aggregate the biogeochemical variables from the PLS scale to the grid cell scale, in which the flux or state is determined by a mean value weighted by the relative abundance of PLSs in that grid cell. For example, the net primary productivity in a grid cell scale () for the grid is

|  |  |  |
| --- | --- | --- |
|  |  | (3) |

Hence, the composition of PLSs and its respective traits in a grid cell directly determines ecosystem scale processes and properties (Fig. 1).

Each functional trait is represented, in a grid cell scale, by an unique mean trait value weighted by the PLSs abundance in the same way as described above for ecosystem processes and properties. This mean value can be understood as the dominant trait value in a community (Díaz et al., 2007)⁠. Then the parameter for each functional trait in a given grid cell is given by

|  |  |  |
| --- | --- | --- |
|  |  | (4) |

where is the value of the functional trait for the respective PLS .

All grid cells are initiated with the same set of PLSs (number and identity) under conditions that are analogous to bare soil. Therefore, even though all trait combinations have equal probability of occupying a given grid cell in the simulation, the PLSs will perform differently such that some strategies will survive while others will be excluded from the spatial grain in the simulation and cannot be reestablished.

*2.2. Simulations setup*

In this study, we employed a non dynamic version of the CAETÊ model, which calculates equilibrium solutions based on long-term mean monthly climate variables from 1980 to 2010 for the Amazon basin (see SM.1.1.c for input data). The model was employed by using two approaches: the PFT-approach, that similar to the majority of vegetation models, used a low functional diversity initialization of 3 PFTs (Table SM.2). While the other approach, TB-approach, used a varying trait-based approach with a high functional diversity initialization of 3000 PLSs (Table SM.3). Other than that, model formulations and principles were the same for both approaches.

We employed six functional traits that were variable between PFTs and PLSs. Since the analysis presented here was focused on the assessment of vegetation carbon storage, three traits represent the carbon allocation percentage of the NPP distributed to different plant tissues, *i.e*., leaves, roots and aboveground woody biomass (hereafter ABGW), and the other three traits represent carbon residence time in the respective plant tissues. Together, these functional traits control the amount of carbon in each plant tissue and the ecophysiological responses to the environment of a PLS or PFT in a daily basis time step..

Three tropical PFTs were defined in the PFT-approach, for which parameters were defined *a priori* using values previously used in other vegetation models (Table SM.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 SM.3. CAETÊ works at a spatial resolution of 0.5º x 0.5º.

*2.3. CAETÊ performance evaluation*

We evaluated and compared the performance of the two approaches (PFT-approach and TB-approach) in representing the spatial distribution of vegetation carbon storage and NPP in the Amazon region in current climatic conditions. We compared our model results with reference data: for carbon storage we used data from Baccini et al. (2012) and Saatchi et al. (2011); for NPP the data were obtained from the MODIS NPP Project (MOD17A3; Running & Zhao, 2021). We considered that 47.5% of living biomass from reference data is comprised by carbon (Thomas & Martin, 2012). It was necessary since CAETÊ simulates the stocks in terms of carbon instead of living biomass, contrary to the data used for comparison. Regarding the carbon, only the aboveground component was considered, as in the data used as reference. For the model performance evaluation we computed the absolute difference between maps of CAETÊ simulation and maps from reference data and also the total carbon stock and NPP for the region.

*2.4. 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 corresponds to the distribution of the mean trait values obtained for each grid cell, as explained in section 2.1. Hence, the trait variation within a grid cell was not considered. Functional diversity and functional composition of communities were regarded here from both the perspective of their single-trait components, *i.e.,* each functional trait independently, and their multi-trait components, *i.e.,* the combination of traits. The single-trait and multi-trait analyses allow the understanding of how the community occupies the functional trait 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 Carmona et al. (2016), emphasizing that each trait value is derived from a grid cell. 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, that is, the so-called trait probability distributions (TPDs). From TPDs, we assessed the three functional diversity components as defined by Carmona et al. (2016): (i) functional richness: the 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 trait values of the PLSs or PFTs in the functional trait space; and (iii) functional divergence: the degree to which the abundance of trait values of PFTs/PLS are distributed toward the extremes of their functional trait space.

For the 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 component metrics. Within such a hypervolume,⁠ functional richness can be interpreted as the amount of volume that is occupied by the community, relative to the potentially available functional space, based on the frequency of trait values that compose 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 detail, see SM.3). Using the factor scores on the chosen principal components (see SM.3), we were able to meet the statistical assumptions for constructing the hypervolume.

*2.5 Decreased precipitation experiment*

In this modeling experiment, we applied a 50% precipitation reduction in the same 1980-2010 monthly climatology used in the control, that is, regular climate conditions. The reduction in precipitation was homogeneous: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 over 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 as a proof of concept and to test our three proposed hypotheses.

For hypothesis H1, we compared the degree of change in carbon stock between the two modeling approaches (TB-approach *vs*. PFT-approach). Then, to understand the role of functional diversity in this change, we assessed whether the plant communities were functionally reorganized by the climatic forcing scenario. For this, we computed the dissimilarities index (degree of overlap) between the TPDs before and after the reduced precipitation for each of the modeling approaches. This index varies from 0 (completely functionally similar) to 1 (completely functionally different) as per Carmona et al., (2016). We also evaluated the changes in hypervolume with precipitation reduction by computing the degree of overlap through the Jaccard similarity index, which ranges from 0 (completely different) to 1 (completely similar). In addition, we compared the degree of centroid displacement between TB-approach and PFT-approach, which indicates how much the mean values of the communities were dislocated from their pre-disturbance location within the hypervolume. This was done by calculating the distance between the centroids before and after the disturbance application.

In order to test the second hypothesis we analyzed the changes in curves generated by the TPDs, *i.e.* we evaluated the change in trait abundance throughout the functional space, showing, for example, the exclusion of trait values and/or the increase in the occurrence of trait values that were rare before the disturbance.

The third hypothesis was tested by accounting for the percentage change of the three facets of functional diversity (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 in volume sizes, which represent a shift in community functional richness. For that, we constructed four hypervolumes using the factor scores of the previously performed PCA, *i.e.*, one for each model approach (TB-approach/PFT-approach) and climatic scenario (regular climate/reduced precipitation). Then, we compared the two hypervolumes of each model approach.

**3. Results**

*3.1. Carbon stocks under reduced precipitation: functional diversity do matter*

The 50% reduction in precipitation caused a widespread carbon stocks depletion along the basin, including total carbon losses in some grid cells in both model approaches (Fig. 2a and b). The total carbon loss was similar between the two modeling approaches (~60%), however, the spatial pattern along the studied region showed clear differences between modeling approaches. The TB-approach was able to maintain carbon stocks in some areas where no PFTs survived in the PFT-approach. This was more evident in the central Amazon and in naturally drier areas, such as the transition between the Amazon forest and the savannah (*Cerrado*) in the southeast region. Furthermore, carbon losses in the TB-approach presented a smoother gradient between a grid cell value and its neighboring cells and across different basin regions, unlike in the PFT-approach, that showed much sharper differences within grid cells. Unexpectedly, in grid cells where both modeling approaches maintained at least a minimum carbon stock, the PFT-approach presented higher values when compared to those from the TB-approach (Fig. 2a and b).

Specific plant compartments showed different patterns of changes when comparing the two modeling approaches (Fig. 2c and d for fine roots, Fig. SM.2 for leaves and ABGW). None of the compartments showed an increase in carbon stock with precipitation reduction, except for the fine roots compartment in the TB-approach (blue areas in Fig. 2d), which was most evident in the transitions from humid and evergreen forest to the Brazilian savannahs and in the northwest region of the basin. The increased investment in fine roots resulted in higher root:shoot ratio in the TB-approach, with an average increase of 74.7%, in contrast to an average decrease of 7.7% for the PFT-approach.

*3.2. Effects of reduced precipitation on functional composition*

For both the PFT-approach and TB-approach, we found high dissimilarity index values (close to 1; Table 1) owing to changes in the TPD distributions (Fig. 3) for the six plant functional traits when applying reduction in precipitation. The dissimilarity indices indicate that the communities significantly changed in terms of its structure and composition after the disturbance application. Trait composition shifted toward lower hyperdominance (decrease in the peaks of the curves) of previously restricted range of values and an increased density of other trait values that were previously rare (very low density) or absent (Fig. 3). Additionally, with the applied change in precipitation, the traits hypervolumes from the TB-approach and the PFT-approach showed a pronounced modification in the way they occupy the functional space (Fig. 4 and SM.6). So that the degree of overlap between the hypervolumes of each modeling approach before and after the disturbance scenario yielded a value of 0.038 for the TB-approach and of 0.009 for the PFT-approach, thus indicating almost no similarity. In addition, the distance between the centroids of the two hypervolumes after imposing a climatic change indicated a change in the mean values and composition; the centroid distance (considering regular climate and low precipitation scenario) was 5.25 for the TB-approach and 0.937 for the PFT-approach.

Regarding the distribution of the traits along the functional space with the reduced precipitation, when considering traits separately, the PFT-approach showed a trimodal distribution, with three clear and discrete peaks along the trait space, but without alteration in the range of values (Fig. 3b, d, f, h, j and l). In the TB-approach, the distribution showed a higher diversity of values with increased density, which resulted in a much more diffuse distribution within the functional space (Fig. 3a, c, e, g, i and k). In general, reduced precipitation in the TB-approach resulted in an increase in density toward higher carbon allocation in fine roots and toward lower carbon allocation in leaves and in ABGW especially (Fig. 3a, c and e ), and an increase in residence time for leaves and fine roots but a decrease for ABGW (Fig. 3g, i and k ). The same pattern distribution along functional space observed for single traits arose when considering all traits combined through the hypervolumes; for the PFT-approach, it was possible to notice three clear data groupings under drought (Fig. 4a) and a much less discretized data distribution from the TB-approach (Fig. 4b).

*3.3. Reduced precipitation impacts on functional diversity facets*

The alterations in the density distribution of functional traits drove changes in the three facets of functional diversity. We found an increase in functional richness for all traits in both approaches, except for residence time in ABGW for the PFT-approach (Fig. 5a). For all the traits in the TB-approach, we observed an increase greater than 100% for functional evenness. In the PFT-approach, the change was the opposite and traits showed a decrease in this functional diversity component, except for allocation and residence time in AGBW (Fig. 5b). Regarding divergence, the TB-approach showed an increase of more than 200% for the leaf allocation trait, while the other TB-approach traits displayed a reduction of this variable (Fig. 5c). The PFT-approach presented an increase in divergence for all functional traits, with the exception of leaf allocation and residence time in ABGW (Fig. 5c). From a multi-trait perspective, we observed an increase in richness, both for the TB-approach and PFT-approach, due to the increase in volume occupied by the communities within the functional space (Fig. 4 and Fig. SM.6). The former presented an increase in the size of the volume to 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 the TB-approach and PFT-approach, respectively, while under reduced precipitation, we found a volume size of 47.84 for the TB-approach and 0.75 for the PFT-approach.

*3.4. CAETÊ model performance evaluation*

We found that both modeling approaches, to some extent, showed disparities in carbon storage and NPP values when compared to the reference data. However, the TB-approach presented a better agreement with reference data for all analyzed variables (Fig. 6).

Within the studied region, regarding total aboveground carbon stock, Baccini et al (2012) estimated 80.2 PgC and Saatchi et al. (2011) estimated 71.7 PgC, while the PFT-approach simulated 127.9 PgC and the TB-approach simulated 86.0 PgC. Then, the TB-approach simulation for total aboveground carbon stock was closer to reference data than the PFT-approach. In terms of spatial patterns in carbon storage, both approaches overestimated the values at the basin edges, and the PFT-approach also tended to overestimate values throughout the Amazon basin, with emphasis on the central region (Fig. 6). On the other hand, the TB-approach tended to underestimate mean carbon values in some regions, for example, in the east and southwest parts of the basin. Even so, the TB-approach presented more areas with no differences between simulated and reference values (white cells in Fig. 6b and e) thereby matching the values used as reference reasonably well.

The CAETÊ model simulated a total annual NPP of 122.3 PgCyr⁻¹ (PFT-approach) and 76.0 PgCyr⁻¹ (TB-approach) for the studied region. Estimates based on MODIS produced a value of 74.6 PgCyr⁻¹ (Running & Zhao, 2021). Thus, the total NPP value simulated by CAETÊ in its trait-based version (TB-approach) was much closer to the value estimated by MODIS. In comparing the NPP simulated by CAETÊ with remote sensing NPP estimations (MODIS; Running & Zhao, 2021), the TB-approach revealed a reasonably good ability to capture broad spatial patterns of remotely sensed NPP estimations (MODIS; Running & Zhao, 2021; Fig. SM.5b), despite an underestimation in the Andean region and a small overestimation in the northwest/central basin region. In contrast, the PFT-approach presented a widespread and prominent overestimation for this variable (Fig. SM.5a), except for the underestimation in the Andean region.

**4. Discussion**

Our results showed that the applied reduced precipitation scenario induced a loss of carbon throughout the study region in both modeling approaches. Despite similar carbon losses among the modeling approaches, we observed more subtle or smoother carbon losses in the TB-approach, which also showed areas where the carbon stock was maintained but where no PFTs were able to survive in the PFT-approach. Carbon stocks were reduced in all of the plant compartments, except for fine roots in the TB-approach, as a response to reduced water availability. Both modeling approaches showed changes in the density distribution curves of traits and in the size of the volume occupied within the functional trait space. Consequently, the three facets of functional diversity were modified (in distinct directions) under reduced precipitation for both modeling approaches but the magnitude of change was higher in the TB-approach. We also found that the TB-approach showed better performance in representing carbon stocks and NPP against estimations/observations compared to the PFT-approach.

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

We found that, in accordance with our first hypothesis and previous literature (Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), the inclusion of trait variability in vegetation models matters for evaluating the impacts of environmental change in ecosystems. Although the two approaches have shown very similar losses when considering the total carbon stock, spatial patterns show that only taking into account the total carbon stock can hide important details of the role of diversity in determining ecosystem functioning. For example, the TB-approach avoided sharp boundaries (especially in naturally) drier regions, showing a more subtle, less sensitive, and probably more realistic, change in carbon stock along the basin (Fig. 2).

It is expected that disturbances, such as reduced precipitation, lead to shifts in the occurrence and abundance of species/functional traits in order to adapt to the new environmental conditions (Aguirre-Gutiérrez et al., 2020; Barros et al., 2016; Esquivel-Muelbert et al., 2019)⁠. Such changes were well captured in our modeling experiment: similarity/dissimilarity indices (for the single and multi-trait perspectives), together with centroid displacements, showed that the functional structure and composition of the plant communities was significantly modified by the climatic forcing scenario. Although both modeling approaches have shown functional restructuration, the ability to functionally reorganize to deal with the new climatic condition was much higher in the model with a more diverse community (TB-approach; Fig. 3), as hypothesized (H1). This result is attributed to the functional density compensation process that counterbalances for losses or decreases in the dominance of strategies, thus ensuring ecosystem functioning or decreasing the impact of disturbance (Gonzalez & Loreau, 2009; Mori et al. 2013; Sakschewski et al., 2016). Once alternative PFTs in the PFT-approach are too low to compensate for losses, it prevents better suited trait combinations to establish, which explain the higher occurrence of grid cells in which none PFT survives (Fig. 2). This sharped and more severe effects of environmental change using a PFT approach is in agreement with other modeling exercises (Huntingford et al., 2013; Sakschewski et al., 2016)⁠. In that sense, our results contribute to reinforcing the importance of functional diversity for maintaining ecosystem functioning and corroborates with the “insurance hypothesis” (Mori, Furukawa, & Sasaki, 2013; Yachi & Loreau, 1999), strengthening the general agreement that diversity promotes ecosystem stability (Tilman et al., 2006).

*4.2. Functional composition and the selection of plant life strategies*

Although the two approaches have shown considerable changes in their functional composition and structure due to reduced precipitation, the degree of these changes differed owing to the distinct abilities to reorganize the community. This difference is supported by the dissimilarity/similarity indexes found between the TPDs and the hypervolumes, respectively, with the reduced precipitation. The distance between the centroids also showed that the mean values (composition) were modified in a higher magnitude for the TB-approach when compared to the PFT-approach approach with reduced precipitation applied. The higher capacity of TB-approach to functionally reorganize enabled community composition changes that corroborates H2: a prioritization of plant strategies with higher fine root allocation and residence time (Fig. 3c and i). This higher investment in roots simulated in the TB-approach was to the detriment of investment in leaves (Fig. 3a and g) and ABGW (Fig. 3e and k), leading to higher root:shoot ratios when compared to the simulations of the TB-approach in regular climate conditions. Higher root biomass enabled water uptake and allowed the community of the TB-approach to better deal with the imposed moisture stress and maintain carbon stocks or reduce the degree of biomass loss. The prioritization of root investment at the expense of other tissues in response to drought has been observed in ecosystem experiments and from forest plot monitoring (Doughty et al., 2014; Kannenberg et al., 2019; Rowland et al., 2014)⁠. As hypothesized (H2), given the limited trait variability, the PFT-approach did not show these changes in carbon investment, increasing mortality rates and preventing the PFTs from establishing in some grid cells, thereby rendering the ecosystem more vulnerable in general (Fig. 2a). Notwithstanding, an unexpected result was that in some grid cells the amount of carbon stock in the PFT-approach was higher than that in the TB-approach with the applied reduced precipitation (Fig. 2a and b). This occurred due increase in the root:shoot ratio in the TB-approach, that is, carbon was allocated toward pools with shorter turnover times (fine roots), which contribute less to total carbon storage than woody tissues (Chave et al., 2009; De Kauwe et al., 2014)⁠. Although the increase in fine roots in the TB-approach provides resistance to moisture stress, thereby preventing the total loss of carbon in several grid-cells, it also led to a lower carbon storage in some locations compared to the PFT-approach. Our findings thus highlight that if the ability to store carbon is used as the only proxy for ecosystem resilience, as is commonly done in currently applied vegetation models, it may result in flawed interpretations on the response of tropical forests to climate change (*e.g*., Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016).

*4.3. Environmental changes modify functional diversity components*

Our results showed that the reduced precipitation modified the way that traits occupy the functional space (Fig. 3 and Fig. 4) and the functional diversity facets (Fig. 5). However, the two modeling approaches employed herein showed distinct results regarding both the direction (except for richness) and magnitude of changes in functional diversity. The distinct results, mainly in the magnitude of change, were derived from the higher ability of the TB-approach to functionally reorganize when compared to the PFT-approach. For example, reduced precipitation led to a wider range of expressed trait values in functional space in the TB-approach, both from a single and multi-trait perspective, thus enabling the occurrence of trait values that were not present before the disturbance or increasing their occurrence (Fig. 3 and Fig. 4) and thus increasing their richness (Fig. 5a). On the other hand, the PFT-approach presented a restricted probability of the occurrence of new trait values, which showed trimodal curves with lower precipitation (Fig. 3), three discrete groups in the hypervolume (Fig. 4) and a lower degree of increase in richness (Fig. 5a).

These results are not in accordance with 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;⁠ Funk et al., 2017; Perronne & Gaba, 2017). However, 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 et al., 1999)⁠. These results provide further evidence that, in some cases, functional richness can increase in disturbance scenarios if environmental change mainly affects the dominant plant strategies (Boersma et al., 2016; Funk et al., 2017; Mouillot et al., 2013).⁠

Additionally, contrary to H3, there was an increased evenness in all considered traits for the TB-approach (Fig. 5b). On the other hand, the PFT-approach showed a decrease in this functional diversity component for most traits (Fig. 5b). The evenness increase in the TB-approach is tightly related to the observed decrease in dominance and increase in the abundance of trait values that were very rare before the disturbance. The decrease in evenness in the 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 two other PFTs. Since the difference between the PFTs was very discretized, the occurrence of trait values concentrated around three peaks of the density distribution function and thus made the distribution less even in the reduced precipitation scenario (Fig. 3b, d, f, h, j and l). Evenness can also be interpreted as evidence of the effectiveness of using the functional niche space⁠; the higher the evenness is, the higher the utilization of the total functional space is (De La Riva et al., 2017; Hillebrand et al., 2008; 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 sensitivity to the applied disturbance, if it presents sufficient variability in its trait values, as we observed for the TB-approach.

Since we expected a more restricted occurrence of trait values with the disturbance application, we assumed an increase in divergence (H3). This means that to address the imposed environmental change, the community would be supported by the increased abundance of more specialist strategies in terms of trait values (Mouillot et al., 2013; Villéger et al., 2010)⁠. However, contrary to our expectations, we observed a general decrease in divergence in the TB-approach (Fig. 5c), which was caused by the strong decrease in abundance of previous dominant trait values, which tended to concentrate at the extremes of functional spaces; consequently, other trait values that were not as abundant became significant for the community after the disturbance. Based on empirical evidence obtained by analyzing a disturbance gradient, Mouillot et al. (2013) also found a decreasing divergence with greater disturbance, which was attributed to declining abundance of the specialist species that were the most impacted by the disturbance. In addition, this decrease in divergence can be 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, the PFT-approach showed a general increase in divergence (Fig. 5c), 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 available trait values, which confers its higher sensitivity to disturbances (Villéger et al., 2010).

*4.5. Model performance*

Our results support the statement that the inclusion of trait variation in vegetation models in fact plays a key role in projecting vegetation carbon cycle. We found that the TB-approach was able to represent NPP and carbon storage reasonably well when compared to references and showed higher agreement than PFT-approach (Fig. 6 and Fig. SM.6). Indeed, the improvement in accuracy in projected biogeochemical variables has already been observed in other studies that added trait variability to existing modelling approaches (Fyllas et al., 2014; Sakschewski et al., 2015; Verheijen et al., 2013). This can be explained by the fact that trait variability confers a higher diversity of community responses to environmental filtering derived from climatic heterogeneity, thereby allowing for a more realistic simulation of the community assembly (Keddy, 1992)⁠.

However, both modeling approaches presented some mismatches with the reference maps. For example, the PFT-approach showed a generalized overestimation of aboveground carbon storage and NPP (Fig. 6 and Fig. SM.6). This result is derived from the fact that the PFTs (chosen from previous PFTs implemented in DGVMs – Dynamic Global Vegetation Models) are already parameterized to present a high performance (or optimal trait combination) in the climatic envelope found in regions dominated by tropical forests, which allowed an elevated occurrence of PFTs with higher carbon storage (Scheiter et al., 2013; Verheijen et al., 2013)⁠.

Additionally, both approaches presented a tendency to overestimate carbon storage and NPP at the edges and in the central/northwestern Amazon basin (Fig. 6 and Fig. SM.6). 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 be linked to the lack of representation of human land use or fire for determining vegetation distribution in the model (Houghton et al., 2001; Saatchi et al., 2007)⁠. Another important caveat of this study is that the model does not yet present a plant hydraulics module, and 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)⁠. Additionally, our model does not consider the effects of biotic interactions, such as mechanistic competition and facilitation, which seem to play a vital role in determining community assembly and ecosystem functioning (Falster et al., 2017; Kunstler et al., 2016; Mori et al., 2013)⁠. Furthermore, nutrient cycling representation (nitrogen and phosphorus) is not represented in our model, what has been shown to be essential for a reliable representation of carbon storage along the Amazon basin (Fleischer et al., 2019)⁠. In that sense, we strongly recommend that further studies using vegetation models, including CAETÊ, aimed at understanding the impacts of moisture stress on the Amazon forest carbon stock should consider land use changes, plant hydraulic traits, biotic interactions and nutrient cycling.

With respect to functional diversity analysis in this study, we considered the whole Amazon basin as a single ecological unit where each grid-cell is represented by one number of trait for each trait considered through a CWM. This metric has been used by several studies that seek to understand the role of functional traits for plant communities (*e.g.,* Díaz et al., 2007; Garnier et al., 2004; Lavorel et al., 2008)⁠ and according to Casanoves et al. (2010) is a good metric to represent the expected value of a functional attribute from a random sample of a community. However, this type of metric may lead to a simplification of diversity within the basin for the TB-approach. 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.

**5. Conclusions**

Despite the development of trait-based vegetation models in the last few decades and its promising potential advantages, few studies thus far have investigated in depth whether the inclusion of trait variability in fact improves the representation of ecosystem properties and processes. Furthermore, the potential of trait-based models to tackle functional ecology-relevant questions, such as the role of functional diversity and its different components in the vulnerability of ecosystems against climate change, has yet to be more deeply explored.

Here we present a novel approach for flexible representation of functional trait variability in vegetation models, the model CAETÊ. In this modeling exercise, We compared, for the first time, (i) how the use of a PFT approach differs from a trait-based approach in terms of the 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 in functional diversity components (richness, evenness and divergence) due to lower water availability are connected to the carbon storage responses of the two modeling approaches.

The use of a PFT and a trait-based approach in the same vegetation model provided a proof of concept on the importance of incorporating trait variability in vegetation models. Our results demonstrated that this incorporation improves accuracy in representing biogeochemical variables. Besides, we also provided modeling evidence that including trait variability is key to capture the vulnerability of ecosystems under climate change.

Moreover, the trait-based method presented herein emphasizes the importance of exploring the impacts of climate change on functional diversity itself and its connection with ecosystem functioning. In that sense, we unexpectedly found that a harsher environment can increase occupation of the functional space. This can be attributed to a reduction in hyperdominance followed by the creation of new functional ecological niches for new combinations of traits, or hitherto rare combinations, thereby promoting an insurance of ecosystem properties. While the limited capacity to change community functional structure with the use of a small number of PFTs overestimates the impacts of environmental changes. Our results showed that trait-based models such as CAETÊ, in its trait-based approach version, in combination with community ecology analysis are important tools for investigating mechanisms and processes that link biodiversity (mainly functional diversity), ecosystem functioning and resilience and can be also further used to investigate other ecological questions such as community assembly rules and biogeographical patterns of functional diversity.

In conclusion, this study demonstrated that the CAETÊ framework for including trait diversity in vegetation models is feasible and can be used in future studies, with enough flexibility to be applied in several climatic scenarios, to use different variable functional traits, and to be broadly applicable to any ecosystem on the planet. Hence, CAETÊ constructs a robust foundation to advance our understanding of the impacts that climate change may pose on hyperdiverse tropical ecosystems such as the Amazon forest.

**CRediT statements**

**Bianca Fazio Rius:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization. **João Paulo Darela Filho:** Software,Methodology, Validation, Formal analysis, Data Curation, Writing - Review & Editing. **Katrin Fleischer:** Conceptualization**,** Writing - Review & Editing. **Florian Hofhansl:** Conceptualization, Writing - Review & Editing. **Carolina Casagrande Blanco:** Conceptualization**,** Writing - Review & Editing. **Tomas Domingues:** Writing - Review & Editing. **Anja Rammig:** Writing - Review & Editing. **David Montenegro Lapola:** Conceptualization, Methodology, Resources, Validation, Writing - Original Draft, Supervision, Project administration, Funding acquisition

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The authors of this manuscript have no conflict of interest to declare.

**Data Availability Statement**

The data that support the findings of this study are openly available in GitHub at<https://github.com/BiancaRius/CAETE_Rius_etal_2021>

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1. Plant functional types [↑](#footnote-ref-1)
2. Represents vegetation through a small number of PFTs (*i.e.,* low functional diversity) [↑](#footnote-ref-2)
3. Trait-based approach: represents vegetation using a high number of trait values combination (*i.e.,* high functional diversity) [↑](#footnote-ref-3)
4. Aboveground woody tissues [↑](#footnote-ref-4)