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

**Authors:** Bianca Fazio Riusa,b,\*, João Paulo Darela Filhoa,c, Katrin Fleischerd,e,, Florian Hofhanslf, Carolina Casagrande Blancoa, Anja Rammige, Tomas Dominguesg,David Montenegro Lapola a,b,c

**Institutional affiliations:**

aUniversity of Campinas (Unicamp) Earth System Science Laboratory, Center for Meteorological and Climatic Research Applied to Agriculture), Campinas - SP, Brazil

bUniversity of Campinas (Unicamp), Biology Institute, Campinas - SP, Brazil

cSão Paulo State University (Unesp), Institute of Biosciences, Rio Claro - SP, Brazil

dMax-Planck-Institute for Biogeochemistry, Department for Biogeochemical Signals, Jena, Germany

eTechnical University of Munich (TUM), School of Life Sciences, Freising, Germany

fInternational Institute for Applied Systems Analysis (IIASA), Biodiversity and Natural Resources Program, Laxenburg, Austria.

gUniversidade de São Paulo (USP), Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Departamento de Biologia, Ribeirão Preto - SP, Brazil

**\*Corresponding author:**

Bianca Fazio Rius

Earth System Science Lab, Center for Meteorological and Climatic Research Applied to Agriculture, University of Campinas (Unicamp), Campinas, 1308-886 - SP, Brazil

Email: [biancafaziorius@gmail.com](mailto:biancafaziorius@gmail.com)

**Highlights**

* We present a novel trait-based model to represent diversity of plant life strategies
* Trait values combinations in a hypervolume create unique plant life strategies
* Trait variability is crucial to Amazon forest vulnerability to reduced precipitation
* Higher functional diversity allows functional reorganization of plant communities

* Different components of functional diversity
* Including trait variability improves representation of plant carbon storage and NPP.

**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 vegetation carbon storage and net primary productivity (NPP) in current climatic conditions and the impacts of plant functional diversity on vegetation carbon storage under low precipitation, by using two approaches: (i) Plant Functional type Approach (PFA) including three PFTs, and (ii) a varying Trait-Based Approach (TBA) including 3000 plant life strategies (PLSs). Six traits were considered: carbon allocation and residence time in leaves, wood, and fine roots. Trait variability improved the model’s performance in representing NPP and vegetation carbon storage in the Amazon. Reduced precipitation caused a similar decrease in total vegetation carbon storage for PFA and TBA (~60%) but carbon loss in the PFA was more homogeneous and widespread across the basin. We found that by accounting for trait variability the plant community was able to functionally reorganize via changes in PLS abundance in the model. Consequently, functional niches were created in the TBA, enabling new/previously rare trait combinations to emerge from the available plant life strategies pool. The TBA yielded strategies that invest more heavily 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 a lower vegetation carbon storage in some grid cells. The use of only three PFTs overestimated the impacts of reduced precipitation in the PFA due to the limited capacity to reorganize the plant functional community. Our findings suggest that plant functional diversity is paramount when evaluating Amazon forest ecosystem sensitivity to climate change. Including trait variability in models may lead to more reasonable future projections, paving the way for a deeper understanding of the role of biodiversity in ecosystem functioning under climate change.

**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 (chapter 4 in IPCC, 2021)⁠, which can induce biodiversity shifts, including changes in functional diversity (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018) and associated effects on vegetation carbon storage (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 vegetation carbon storage remains poorly understood (Esquivel-Muelbert et al., 2017; 2018; Poorter et al., 2015; Sakschewski et al., 2016).

Due to differences in life-history strategies among plants (Adler et al., 2014), Functional diversity plays a vital role in determining ecosystems functioning and its responses to disturbances (Díaz & Cabido, 2001; Song et al., 2014; Cadotte, 2017). Ultimately, it is the functional traits that delineates plant communities which in turn respond to biotic and abiotic conditions and also shapes ecosystem processes and properties such as vegetation 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). The “insurance hypothesis”, for example, postulates that a higher diversity (richness) of plant strategies (and associated plant functional traits) provides higher variability of responses under new environmental conditions (Mori et al., 2013; Yachi & Loreau, 1999), thus maintaining 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 which enables the functional composition of a community to reorganize and adjust to new environmental conditions, thus 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 may 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 (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 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)⁠, the most likely strategy would be the one that invests more carbon to fine root production to acquire the most limiting resource, in this case, water. 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; Lapola et al., 2009 ⁠)⁠ and an abrupt replacement of the dominant humid tree cover with more arid-affiliated vegetation in large parts of Amazon forests (Hutyra et al., 2005; Salazar et al., 2007). One of the causes that may contribute to such projections is the represention of diversity of plants in models (Pavlick et al., 2013; Scheiter et al., 2013)⁠. Commonly, models represent vegetation based on a very small and discrete set of PFTs[[1]](#footnote-2) 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 reality in these ecosystems is strongly simplified. As a consequence, alternative trait combinations that could perform differently in a changing environment and could better handle new conditions are limited by the small number of PFTs in the models (Fyllas et al., 2014; Mori et al., 2013; Sakschewski et al., 2016)⁠. Then, important mechanisms for resilience, such as functional reorganization (Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), are very restricted in such model approaches, if captured at all. That may be hampering vegetation models to accurately project the impacts of environmental changes in terrestrial ecosystems and may overestimate these impacts (Pavlick et al., 2013; Sakschewski et al., 2016; Verheijen et al., 2015).

In an attempt to overcome these limitations of underrepresenting functional diversity with PFTs, the 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 small number of PFTs with a a richer representation of functional diversity increasing in several times (one to three orders of magnitude higher) the possible functional traits combinations (Pavlicket al., 2013⁠; Reu et al., 2014; Webb et al., 2010; Wullschleger et al., 2014). It also provide a provide the opportunity to explore multiple functional ecology-related questions in combination with biogeochemical fluxes and pools (Sakschewski et al., 2016; Darela-Filho et al., in prep.)⁠. Trait-based vegetation models may explore the role of different components of functional diversity on ecosystem functions, and the processes that determine community assemblage and structure, and how both are affected and interact with environmental changes (Mason et al., 2005; Mouillot et al., 2013b; Song et al., 2014).

Nonetheless many of these functional ecological aspects highlighted in the scientific literature remain underexplored by the modeling community (but see: Hofhansl et al., 2021⁠). 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., 2013b)⁠, the ability of trait-based models to effectively capture (and improve) associated plant functional responses to environmental changes has yet to be tested.

Here we present a new trait-based model, the so-called CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model. To assess the effect of trait variability inclusion in vegetation models we compare two approaches of CAETÊ: a standard PFT approach[[2]](#footnote-3) (hereafter PFA) and a varying trait-based approach[[3]](#footnote-4) (hereafter TBA). Six traits are used to characterize vegetation: as either f: carbon allocation and residence time in three plant compartments (leaves, wood and fine roots). We compared the modelling approaches performance in representing vegetation carbon storage and NPP for the Amazon basin region in order to evaluate whether traits diversity in fact improves the representation of these biogeochemical variables. We further applied a modeled scenario of reduced precipitation in the study area with both modeling approaches, with the intent to evaluate (i) how moisture deficits affect modeled functional composition and functional diversity components (namely, richness, evenness and divergence) and (ii) how these shifts in functional diversity affect Amazon vegetation carbon stocks. Therefore, we hypothesize that in a scenario of reduced precipitation, the approach with higher trait variability (TBA) will present higher ability to maintain carbon vegetation stocks, in line with a less sensitive ecosystem vegetation , due to functional reorganization of plant communities though prioritization of strategies with higher investment in root tissues, which increase water uptake. This functional reorganization would culminate in a more restricted range of functional traits values (*i.e.*, lower functional richness; Cornwell et al., 2006; Funk et al., 2017; Kleidon et al., 2009), although with less regularly distributed densities (*i.e*., lower functional evenness), concentrated towards the extremes of the range (*i.e*., higher functional divergence; Mouillot et al., 2013a; 2011), and hence with a 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 a brief overview of the CAETÊ model (see in-depth model description in Supplementary Material SM.1). In its TBA, 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.1.1.1.). The volume occupied by all possible combinations 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 PLS describe its ecophysiological behavior and its relationship with the environment. For example, each PLS, as a differential combination of functional traits, constitutes a differential way of storing carbon and capturing water and light. Therefore, the functional traits of a plant strategy ultimately determine its performance in a grid cell (abundance and presence/absence). Differential survival and abundance between PLSs are 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 the 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 upscale 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 a unique value, which is the summation of each PLS trait value weighted by the PLS abundance (Eq. 4). This community weighted 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 initialized 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 (Fig. SM.1) at a spatial resolution of 0.5º x 0.5º (see SM.1.2. for input data). The model was employed in two approaches: the PFA, which used a low functional diversity initialization of 3 PFTs (Table SM.2). While the TBA used a high functional diversity initialization of 3000 PLSs (Table SM.3). Otherwise, model process formulations and principles were the same for both approaches.

We employed six functional traits for the definition of PFTs and PLSs. Since the analysis presented here was focused on the assessment of vegetation carbon storage, three traits represented the carbon allocation percentage of the NPP distributed to different plant tissues (namely leaves, roots and wood), and the other three traits represented 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 PFA, for which parameters were set using values adopted from previous vegetation models (Table SM.2). For the TBA, the initial range of values used to create the hypervolume was predefined (Table SM.3).

*2.3. CAETÊ performance evaluation*

We evaluated and compared the performance of the two approaches (PFA and TBA) 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 vegetation 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 from 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 dominant trait values obtained for each grid cell, as explained in section 2.1 (Eq. 4). 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(each functional trait independently), and their multi-trait components (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, that is, 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, that is, 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 fulfill 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 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 hypotheses.

We first compared the degree of change in carbon stock between the two modeling approaches (TBA *vs*. PFA). 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 dissimilarity 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; overlapping density curves) to 1 (completely functionally different; no overlap) 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; no overlap) to 1 (completely similar, overlapping hypervolumes). In addition, we compared the degree of centroid displacement between TBA and PFA, 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 degree of communities’ functional reorganization we analyzed the changes in curves generated by the TPDsbyevaluating the change in trait abundance throughout the functional space, and showing, for example, the exclusion of trait values and/or the increase in the occurrence of trait values that were rare before the disturbance.

We also tested how functional divergence changed by accounting for the percentage change of its 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 (TBA/PFA) 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*

The 50% reduction in precipitation caused a widespread decrease in carbon stocks throughout the basin, in both model approaches (Fig. 2a and b). Total carbon (sum of carbon in all three plant compartments) loss was similar between the two modeling approaches (~60%), however, the spatial pattern of change was different between modeling approaches. The TBA was able to maintain carbon stocks in some areas where no PFTs survived in the PFA. This was more evident in the central Amazon and in naturally drier areas, such as in the transition between the Amazon forest and the Cerrado savannah in the southeast. Furthermore, carbon losses in the TBA presented a smoother gradient between a grid cell value and its neighboring cells and across different basin regions, unlike in the PFA, that showed much sharper differences within grid cells. Surprisingly, in grid cells where both modeling approaches maintained at least a minimum carbon stock, the PFA presented higher values when compared to those from the TBA (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 wood). None of the compartments showed an increase in carbon stock with precipitation reduction, except for the fine roots compartment in the TBA (blue areas in Fig. 2d), an increase which was more evident in the transition between the Amazon and Cerrado and in the northeast part of the basin. The increased investment in fine roots resulted in higher root:shoot ratio in the TBA, with an average increase of 74.7%, in contrast to an average decrease of 7.7% for the PFA.

*3.2. Effects of reduced precipitation on functional composition*

For both the PFA and TBA, 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 TBA and the PFA showed a pronounced modification in the way they occupy the functional space (Fig. 4 and Fig. 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 TBA and of 0.009 for the PFA, 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 TBA and 0.937 for the PFA.

Regarding the distribution of the traits along the functional space with the reduced precipitation, when considering traits separately, the PFA showed a trimodal distribution, with three distinct peaks along the trait space, but without alteration in the range of values (Fig. 3b, d, f, h, j and l). In the TBA, 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 TBA resulted in an increase in density toward higher carbon allocation in fine roots and toward lower carbon allocation in leaves and in wood especially (Fig. 3a, c and e ), and an increase in residence time for leaves and fine roots but a decrease for wood (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 PFA, it was possible to notice three clear data groupings under reduced precipitation (Fig. 4a) and a much less discretized data distribution from the TBA (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 wood for the PFA (Fig. 5a). For all the traits in the TBA, we observed an increase greater than 100% for functional evenness. In the PFA, 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 TBA showed an increase of more than 200% for the leaf allocation trait, while the other TBA traits displayed a reduction of this functional component (Fig. 5c). The PFA presented an increase in divergence for all functional traits, with the exception of leaf allocation and residence time in wood (Fig. 5c). From a multi-trait perspective, we observed an increase in richness, both for the TBA and PFA, due to the increase in volume occupied by the communities within the functional space (Fig. 4 and Fig. SM.6). The TBA presented an increase in the size of the volume to a higher degree than the PFA: Under current climatic conditions, the size of the volume that the data occupied was equal to 1.71 and 0.007 for the TBA and PFA, respectively, while under reduced precipitation, we found a volume size of 47.84 for the TBA and 0.75 for the PFA.

*3.4. CAETÊ model performance evaluation*

We found that both modeling approaches, showed differences in vegetation carbon storage and NPP values when compared to the reference data, while overall, the TBA presented a better agreement for all analyzed variables (Fig. 6).

Within the studied region, regarding, Baccini et al (2012) estimated 80.2 Pg C of total aboveground carbon stock and Saatchi et al. (2011) estimated 71.7 Pg C, while the PFA simulated 127.9 Pg C and the TBA simulated 86.0 Pg C. Then, the TBA simulation for total aboveground carbon stock was closer to reference data than the PFA. In terms of spatial patterns in vegetation carbon storage, both approaches overestimated the values at the basin edges, and the PFA also tended to overestimate values throughout the Amazon basin, with emphasis on the central region (Fig. 6). On the other hand, the TBA tended to underestimate mean carbon values in some regions, for example, in the east and southwest parts of the basin. Even so, the TBA 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 Pg C yr⁻¹ (PFA) and 76.0 Pg C yr⁻¹ (TBA) for the studied region. MODIS-based estimation is 74.6 Pg C yr⁻¹ (Running & Zhao, 2021). Thus, the total NPP value simulated by CAETÊ in the TBA was much closer to the value estimated by MODIS. By comparing the NPP simulated by CAETÊ with remote sensing NPP estimations (MODIS; Running & Zhao, 2021), the TBA 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 PFA presented a widespread and prominent overestimation for this variable (Fig. SM.5a), except for the underestimation in the Andean region.

**4. Discussion**

*4.1. Reduced precipitation impacts on vegetation carbon storage: comparing a PFT with a trait-based approach*

We found that, in accordance with our hypothesis and previous literature (Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), the inclusion of trait variability in vegetation models in fact matters for evaluating the impacts of environmental change in ecosystems. Although the two modelled approaches have shown very similar losses when considering the total carbon stock, spatial patterns showed 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 TBA avoided sharp boundaries (especially in naturally) drier regions, showing a more subtle, less sensitive, and probably more realistic, change in carbon stock across 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 to adapt to the new environmental conditions (Aguirre-Gutiérrez et al., 2020; Barros et al., 2016; Esquivel-Muelbert et al., 2018)⁠. 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 and cope with new climatic conditions was much higher in the model with a more diverse community (TBA; Fig. 3), as hypothesized. 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 PFA are too few to compensate for losses, it prevents better suited trait combinations to establish, which therefore explains the higher occurrence of grid cells in which none PFT survived (Fig. 2). This sharp response and more severe effect of environmental change using a PFT approach agrees 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), thus strengthening the assumption 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 dominant values (composition) were modified in a higher magnitude for the TBA when compared to the PFA approach when reduced precipitation was applied. The higher capacity of TBA to functionally reorganize enabled community composition changes that corroborates our hypothesis: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 TBA was to the detriment of investment in leaves (Fig. 3a and g) and wood (Fig. 3e and k), leading to higher root:shoot ratios when compared to the simulations of the TBA in regular climate conditions. Higher root biomass enabled water uptake and allowed the community of the TBA 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)⁠. Given the limited trait variability, the PFA 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), as predicted. Notwithstanding, an unexpected result was that in some grid cells the amount of carbon stock in the PFA was higher than that in the TBA with the applied reduced precipitation (Fig. 2a and b). This occurred due increase in the root:shoot ratio in the TBA, that is, carbon was allocated toward pools with shorter turnover times (fine roots), which contribute less to total vegetation carbon storage than woody tissues (Chave et al., 2009; De Kauwe et al., 2014)⁠. Although the increase in fine roots in the TBA provides resistance to moisture stress, thereby preventing the total loss of carbon in several grid-cells, it also led to a lower vegetation carbon storage (in some locations) compared to the PFA. Our findings thus highlight that if the total vegetation carbon storage frente a um disturbio alone does not completely indicate tell you about ecosystem functions, or underlying changes in different pools and fluxes.

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, as consequence, 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 TBA to functionally reorganize when compared to the PFA. For example, reduced precipitation led to a wider range of expressed trait values in functional space in the TBA, 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 PFA 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 expectations: 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., 2013a).

Also contrary to our hypothesis, there was an increased evenness in all considered traits for the TBA (Fig. 5b). On the other hand, the PFA showed a decrease in this functional diversity component for most traits (Fig. 5b). The evenness increase in the TBA 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., 2011a)⁠. 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, thus providing a lower sensitivity to the applied disturbance, if the community presents sufficient variability in its trait values, as we observed for the TBA.

Since we expected a more restricted occurrence of trait values with the disturbance application, we assumed an increase in divergence. 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., 2013a; Villéger et al., 2010)⁠. However, unexpectedly, we observed a general decrease in divergence in the TBA (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. (2013a) 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 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, the PFA showed a general increase in divergence (Fig. 5c), and an improvement in the occupation of functional space (low divergence) is impossible considering thelow diversity of available trait values, which confers its higher sensitivity to disturbances (Villéger et al., 2010).

*4.5. Model performance*

Our results indicate that the inclusion of trait variation in vegetation models in fact plays a key role in projecting vegetation carbon cycle. We found that the TBA simulations could represent NPP and vegetation carbon storage reasonably well when compared to references and showed higher agreement than PFA (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 PFA generally showed an overestimation of aboveground vegetation carbon storage and NPP (Fig. 6 and Fig. SM.6). This is due to the fact that the PFTs (chosen from previous PFTs implemented in other 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 a more frequent occurrence of PFTs with higher vegetation carbon storage (Scheiter et al., 2013; Verheijen et al., 2013)⁠.

Additionally, both approaches presented a tendency to overestimate vegetation 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 (but see: 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 were shown 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, but has been found essential for reliably representing vegetation carbon storage across the Amazon basin (Fleischer et al., 2019)⁠.

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 fixed value for each trait considered through a community weighted mean. 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 TBA. 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. We here showed that applying this framework in vegetation models allows investigating plant functional diversity under current and future climatic conditions, and therefore advancing our understanding of biodiversity-ecosystem functioning relationships across the Amazon basin.

**5. Conclusions**

*We here showed that applying this framework in vegetation models allows investigating plant functional diversity under current and future climatic conditions, and therefore advancing our understanding of biodiversity-ecosystem functioning relationships across the Amazon basi**n.*

*In that sense, we strongly recommend that further studies using vegetation models, including CAETÊ, aim 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.*

*Hence, the observed spatial differences identified by each of the applied modeling approaches were associated with differences in trait density distribution and the size of volume occupied within the functional trait space when applied the precipitation scenario.*  This may have implications for modeling the so-called Amazon tipping point (Lovejoy and Nobre 2018), while a TBA-like approach would yield more subtle, but not necessarily less relevant, responses of the forest vegetation to extreme climate change (Sakschewski et a l. 2015).

In contrast, the PFA showed a general increase in divergence (Fig. 5c), and an improvement in the occupation of functional space (low divergence) is impossible considering thelow diversity of available trait values, which confers its higher sensitivity to disturbances (Villéger et al., 2010).

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 really improves the representation of ecosystem properties and processes. Furthermore, the potential of trait-based models to tackle functional ecology-related 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.

The use of a PFT and an approach based on variable traits 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 version that considers variable traits, 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.

**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

**Acknowledgments**

This study has been financed by Sao Paulo Research Foundation – FAPESP through grants to BFR (2019/04223-0), JPDF (2017/00005-3), and DML (2015/02537-7), related to the AmazonFACE∫ME project (labterra.cpa.unicamp.br/amazonface-me/). This study was also financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 88887.177275/2018-00. KF acknowledges funding by the DFG project R2060/5-1.

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>

**References**

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., … Malhi, Y. S. (2019). Drier tropical forests are susceptible to functional changes in response to a long- term drought. *Ecology Letters*, 855–865. https://doi.org/10.1111/ele.13243

Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe, D., … Houghton, R. A. (2012). Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Clim. Change*, *2*(3), 182–185. https://doi.org/10.1038/nclimate1354

Barros, C., Thuiller, W., Georges, D., Boulangeat, I., & Münkemüller, T. (2016). N-dimensional hypervolumes to study stability of complex ecosystems. *Ecology Letters*, *19*(7), 729–742. https://doi.org/10.1111/ele.12617

Blonder, B. (2017). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, (August), 1–13. https://doi.org/10.1111/ecog.03187

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, *23*(5), 595–609. https://doi.org/10.1111/geb.12146

Boersma, K. S., Dee, L. E., Miller, S. J., Bogan, M. T., Lytle, D. A., & Gitelman, A. I. (2016). Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework. *Ecology*, *97*(3), 583–593. https://doi.org/10.1890/15-0688

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>

Cadotte, M. W. (2017). Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters*, *20*(8), 989–996. https://doi.org/10.1111/ele.12796

Cannell, M. G. R., & Dewar, R. C. (1994). *Carbon Allocation in Trees - a Review of Concepts for Modeling*. *Advances in Ecological Research* (Vol. 25). https://doi.org/10.1016/s0065-2504(08)60213-5

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology and Evolution*, *31*(5), 382–394. https://doi.org/10.1016/j.tree.2016.02.003

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2019). Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. *Ecology*, *100*(12), 1–8. https://doi.org/10.1002/ecy.2876

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A Trait-Based Test for Habitat Filtering: Convex Hull Volume. *Source: Ecology Ecology*, *87*(876), 1465–1471. Retrieved from <http://www.jstor.org/stable/20069097>

Cox, P M, Betts, R. a, Jones, C. D., Spall, S. a, & Totterdell, I. J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, *408*(6809), 184–187. https://doi.org/10.1038/35041539

Cox, Peter M., Betts, R. a., Collins, M., Harris, P. P., Huntingford, C., & Jones, C. D. (2004). Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology*, *78*(1–3), 137–156. https://doi.org/10.1007/s00704-004-0049-4

Da Costa, A. C. L., Galbraith, D., Almeida, S., Portela, B. T. T., da Costa, M., de Athaydes Silva Junior, J., … Meir, P. (2010). Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, *187*(3), 579–591. <https://doi.org/10.1111/j.1469-8137.2010.03309.x>

De Bello, F., Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., … Lepš, J. (2021). Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology and Evolution*, *36*(9), 822–836. https://doi.org/10.1016/j.tree.2021.05.001

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y. P., … Norby, R. J. (2014). Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites. *New Phytologist*, *203*(3), 883–899. https://doi.org/10.1111/nph.12847

De La Riva, E. G., Lloret, F., Pérez-Ramos, I. M., Marañón, T., Saura-Mas, S., Díaz-Delgado, R., & Villar, R. (2017). The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events. *Journal of Plant Ecology*, *10*(2), 281–293. https://doi.org/10.1093/jpe/rtw027

Diaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*(1), 113–122. <https://doi.org/10.2307/3237229>

Díaz, S., & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Proceedings. Biological Sciences / The Royal Society*, *16*(4), 646–655. https://doi.org/10.1098/rspb.2010.1923

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., … Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, *3*(9), 2958–2975. https://doi.org/10.1002/ece3.601

Doughty, C. E., Malhi, Y., Araujo-Murakami, A., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., … Ledezma, R. (2014). Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought. *Ecology*, *95*(8), 2192–2201. https://doi.org/10.1890/13-1507.1

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huasco, W. H., … Malhi, Y. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541), 78–82. <https://doi.org/10.1038/nature14213>

Eller, C. B., Barros, F. de V., Bittencourt, P. R. L., Rowland, L., Mencuccini, M., & Oliveira, R. S. (2018). Xylem hydraulic safety and construction costs determine tropical tree growth. *Plant Cell and Environment*, *41*(3), 548–562. <https://doi.org/10.1111/pce.13106>

Enquist, B. J., & Enquist, C. A. F. (2011). Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology*, *17*(3), 1408–1424. https://doi.org/10.1111/j.1365-2486.2010.02326.x

Enquist, B. J., Bentley, L. P., Shenkin, A., Maitner, B., Savage, V., Michaletz, S., … Malhi, Y. (2017). Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Global Ecology and Biogeography*, *26*(12), 1357–1373. <https://doi.org/10.1111/geb.12645>

Esquivel-Muelbert, A., Galbraith, D., Dexter, K. G., Baker, T. R., Lewis, S. L., Meir, P., … Phillips, O. L. (2017). Biogeographic distributions of neotropical trees reflect their directly measured drought tolerances. *Scientific Reports*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-08105-8

Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., … Phillips, O. L. (2018). Compositional response of Amazon forests to climate change. *Global Change Biology*, (June 2018), 39–56. https://doi.org/10.1111/gcb.14413

Falster, D. S., Brännström, Å., Westoby, M., & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, *114*(13), E2719–E2728. <https://doi.org/10.1073/pnas.1610206114>

Fauset, S., Baker, T. R., Lewis, S. L., Feldpausch, T. R., Affum-Baffoe, K., Foli, E. G., … Etienne, R. (2012). Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2012.01834.x

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo M., A., Brienen, R. J. W., … Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, *6*, 6857. https://doi.org/10.1038/ncomms7857

Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., … Lapola, D. M. (2019). Amazon forest response to CO2 fertilization dependent on plant phosphorus acquisition. *Nature Geoscience*, *12*(9), 736–741. https://doi.org/10.1038/s41561-019-0404-9

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., … Wright, J. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*, *92*(2), 1156–1173. https://doi.org/10.1111/brv.12275

Fyllas, N. M., Gloor, E., Mercado, L. M., Sitch, S., Quesada, C. a., Domingues, T. F., … Lloyd, J. (2014). Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v.1). *Geoscientific Model Development*, *7*, 1251–1269. <https://doi.org/10.5194/gmd-7-1251-2014>

Galbraith, D., Levy, P. E., Sitch, S., Huntingford, C., Cox, P., Williams, M., & Meir, P. (2010). Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *The New Phytologist*, *187*, 647–665. https://doi.org/10.1111/j.1469-8137.2010.03350.x

Gamfeldt, L., Hillebrand, H., & Jonsson, P. R. (2008). Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology*, *89*(5), 1223–1231. <https://doi.org/10.1890/06-2091.1>

Gonzalez, A., & Loreau, M. (2009). The Causes and Consequences of Compensatory Dynamics in Ecological Communities. *Annu.Rev.Ecol.Syst.*, *40*, 393–414. https://doi.org/10.1146/annurev.ecolsys.39.110707.173349

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of Dominance: a Review of Evenness Effects on Local and Regional Ecosystem Processes. *Ecology*, *89*(6), 1510–1520. https://doi.org/10.1890/07-1053.1

Hofhansl, F., Chacón‐Madrigal, E., Brännström, Å., Dieckmann, U., & Franklin, O. (2021). Mechanisms driving plant functional trait variation in a tropical forest. *Ecology and Evolution*. https://doi.org/10.1097/bot.0000000000002145

Houghton, R. a, Lawrence, K. T., Hackler, J. L., & Brown, S. (2001). The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, *7*(7), 731–746. https://doi.org/DOI 10.1046/j.1365-2486.2001.00426.x

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. <https://doi.org/10.1038/s41586-020-2035-0>

Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L. M., Sitch, S., Fisher, R., … Cox, P. M. (2013). Simulated resilience of tropical rainforests to CO2-induced climate change. *Nature Geoscience*, *6*(4), 268–273. <https://doi.org/10.1038/ngeo1741>

Hutyra, L. R., Munger, J. W., Nobre, C. A., Saleska, S. R., Vieira, S. A., & Wofsy, S. C. (2005). Climatic variability and vegetation vulnerability in Amazǒnia. *Geophysical Research Letters*, *32*(24), 1–4. <https://doi.org/10.1029/2005GL024981>

IPCC, 2021: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu,and B. Zhou (eds.)]. Cambridge University Press. In Press.

Joshi, J., Stocker, B. D., Hofhansl, F., Zhou, S., Dieckmann, U., & Prentice, I. C. (2020). Towards a unified theory of plant photosynthesis and hydraulics. *BioRxiv*. https://doi.org/10.1101/2020.12.17.423132

Kannenberg, S. A., Novick, K. A., Alexander, M. R., Maxwell, J. T., Moore, D. J. P., Phillips, R. P., & Anderegg, W. R. L. (2019). Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. *Global Change Biology*, *25*(9), 2978–2992. https://doi.org/10.1111/gcb.14710

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, *3*(2), 157–164. https://doi.org/10.2307/3235676

Kleidon, A., Adams, J., Pavlick, R., & Reu, B. (2009). Simulated geographic variations of plant species richness, evenness and abundance using climatic constraints on plant functional diversity. *Environmental Research Letters*, *4*(1), 014007. <https://doi.org/10.1088/1748-9326/4/1/014007>

Koch, A., Hubau, W., & Lewis, S. L. (2021). Earth System Models Are Not Capturing Present-Day Tropical Forest Carbon Dynamics. *Earth’s Future*, *9*(5), 1–19. https://doi.org/10.1029/2020EF001874

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, Robert, M., Laughlin, D. C., … Ruiz-Benito, P. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*(7585), 1–15. <https://doi.org/10.1038/nature16476>

Lapola, D. M., Oyama, M. D., & Nobre, C. A. (2009). Exploring the range of climate biome projections for tropical South America: The role of CO2 fertilization and seasonality. *Global Biogeochemical Cycles*, *23*(3), 1–22. https://doi.org/10.1029/2008GB003357

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisting the Holy Grail. *Functional Ecology*, *16*(Essay Review), 545–556. https://doi.org/Doi 10.1046/J.1365-2435.2002.00664.X

Levine, N. M., Zhang, K., Longo, M., Baccini, A., Phillips, O. L., Lewis, S. L., … Moorcroft, P. R. (2016). Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences*, *113*(3), 793–797. https://doi.org/10.1073/pnas.1511344112

Lohbeck, M., Bongers, F., Martinez-Ramos, M., & Poorter, L. (2016). The importance of biodiversity and dominance for multiple ecosystem functions in a human- modified tropical landscape. *Ecology*, *97*(10), 2772–2779. Retrieved from http://onlinelibrary.wiley.com/journal/10.1002/(ISSN)1939-9170/issues

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Metcalfe, D. B., Meir, P., Aragão, L. E. O. C., Lobo-do-Vale, R., Galbraith, D., Fisher, R. A., … Williams, M. (2010). Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytologist*, *187*(3), 608–621. https://doi.org/10.1111/j.1469-8137.2010.03319.x

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, *88*(2), 349–364. <https://doi.org/10.1111/brv.12004>

Mouchet, M. a., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., … Thuiller, W. (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biology*, *11*(5). https://doi.org/10.1371/journal.pbio.1001569

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N. W. H. (2011). Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, *6*(3). https://doi.org/10.1371/journal.pone.0017476

Papastefanou, P., Zang, C. S., Pugh, T. A. M., Liu, D., Grams, T. E. E., Hickler, T., & Rammig, A. (2020). A Dynamic Model for Strategies and Dynamics of Plant Water-Potential Regulation Under Drought Conditions. *Frontiers in Plant Science*, *11*(April), 1–13. https://doi.org/10.3389/fpls.2020.00373

Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., & Kleidon, A. (2013). The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences*, *10*(6), 4137–4177. https://doi.org/10.5194/bg-10-4137-2013

Perronne, R., & Gaba, S. (2017). How to design trait-based analyses of community assembly mechanisms : Insights and guidelines from a literature review, *25*, 29–44. https://doi.org/10.1016/j.ppees.2017.01.004

Phillips, O. L., Heijden, G. Van Der, Lewis, S. L., Lo, G., Lloyd, J., Malhi, Y., … Silva, J. (2010). Drought–mortality relationships for tropical forests. *New Phytologist*, *187*, 631–646.

Poorter, L., van der Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcón, A., Álvarez-Sánchez, J., … Peña-Claros, M. (2015). Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography*, *24*(11), 1314–1328. <https://doi.org/10.1111/geb.12364>

Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., … Sykes, M. T. (2007). Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change. *Terrestrial Ecosystems in a Changing World*, 175–192. <https://doi.org/10.1007/978-3-540-32730-1_15>

Rammig, A., Jupp, T., Thonicke, K., Tietjen, B., Heinke, J., Ostberg, S., … Shukla, J. (2010). Amazon deforestation and climate change. *Global Change Biology*, *4*(3), 957–988. https://doi.org/10.1111/j.1365-2486.2009.02157.x

Reu, B., Proulx, R., Bohn, K., Dyke, J. G., Kleidon, A., Pavlick, R., & Schmidtlein, S. (2011). The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. *Global Ecology and Biogeography*, *20*(4), 570–581. <https://doi.org/10.1111/j.1466-8238.2010.00621.x>

Reu, B., Zaehle, S., Bohn, K., Pavlick, R., Schmidtlein, S., Williams, J. W., & Kleidon, A. (2014). Future no-analogue vegetation produced by no-analogue combinations of temperature and insolation. *Global Ecology and Biogeography*, *23*(2), 156–167. https://doi.org/10.1111/geb.12110

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., … Meir, P. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, 1–13. https://doi.org/10.1038/nature15539

Rowland, Lucy, Hill, T. C., Stahl, C., Siebicke, L., Burban, B., Zaragoza-Castells, J., … Williams, M. (2014). Evidence for strong seasonality in the carbon storage and carbon use efficiency of an Amazonian forest. *Global Change Biology*, *20*(3), 979–991. <https://doi.org/10.1111/gcb.12375>

Running, S., Zhao, M. (2021). *MODIS/Terra Net Primary Production Gap-Filled Yearly L4 Global 500m SIN Grid V061* [Data set]. NASA EOSDIS Land Processes DAAC. Accessed 2021-09-01 from https://doi.org/10.5067/MODIS/MOD17A3HGF.061

Saatchi, S., Houghton, R. A., Dos Santos Alval??, R. C., Soares, J. V., & Yu, Y. (2007). Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology*, *13*(4), 816–837. https://doi.org/10.1111/j.1365-2486.2007.01323.x

Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., … Morel, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, *108*(24), 9899–9904. https://doi.org/10.1073/pnas.1019576108

Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., … Thonicke, K. (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*, *1*(August). https://doi.org/10.1038/nclimate3109

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., … Thonicke, K. (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, 2711–2725. <https://doi.org/10.1111/gcb.12870>

Salazar, L. F., Nobre, C. A., & Oyama, M. D. (2007). Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, *34*(9), 2–7. https://doi.org/10.1029/2007GL029695

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: learning from community ecology. *The New Phytologist*. https://doi.org/10.1111/nph.12210

Schmitt, S., Maréchaux, I., Chave, J., Fischer, F. J., Piponiot, C., Traissac, S., & Hérault, B. (2019). Functional diversity improves tropical forest resilience: Insights from a long-term virtual experiment. *Journal of Ecology*, (October), 1–13. <https://doi.org/10.1111/1365-2745.13320>

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., … Woodward, F. I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, *14*(9), 2015–2039. https://doi.org/10.1111/j.1365-2486.2008.01626.x

Song, Y., Wang, P., Li, G., & Zhou, D. (2014). Relationships between functional diversity and ecosystem functioning: A review. *Acta Ecologica Sinica*, *34*(2), 85–91. <https://doi.org/10.1016/j.chnaes.2014.01.001>

Thomas, S. C., & Martin, A. R. (2012). Carbon content of tree tissues: A synthesis. *Forests*, *3*(2), 332–352. https://doi.org/10.3390/f3020332

Thornley, J. H. M. (1972). A balanced quantitative model for root: Shoot ratios in vegetative plants. *Annals of Botany*, *36*(2), 431–441. https://doi.org/10.1093/oxfordjournals.aob.a084602

Verheijen, L. M., Brovkin, V., Aerts, R., Bönisch, G., Cornelissen, J. H. C., Kattge, J., … Van Bodegom, P. M. (2013). Impacts of trait variation through observed trait-climate relationships on performance of an Earth system model: A conceptual analysis. *Biogeosciences*, *10*(8), 5497–5515. <https://doi.org/10.5194/bg-10-5497-2013>

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J., & van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology*, 3074–3086. https://doi.org/10.1111/gcb.12871

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *America*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomie vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, *20*(6), 1512–1522. <https://doi.org/10.1890/09-1310.1>

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Walker, B., Kinzig, A., & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems*, *2*(2), 95–113. https://doi.org/10.1007/s100219900062

Webb, C. T., Hoeting, J. a., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, *13*(3), 267–283. <https://doi.org/10.1111/j.1461-0248.2010.01444.x>

Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., … Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences*, *116*(15), 7591–7591. <https://doi.org/10.1073/pnas.1904390116>

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., … Xu, X. (2014). Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, *114*(1), 1–16. https://doi.org/10.1093/aob/mcu077

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

1. Plant functional types [↑](#footnote-ref-2)
2. Represents vegetation through a small number of PFTs (*i.e.,* low functional diversity) [↑](#footnote-ref-3)
3. Represents vegetation using a high number (3000) of trait values combination that represent plant life strategies (*i.e.,* high functional diversity) [↑](#footnote-ref-4)