**Title:**

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

**Including trait variability improves accuracy in carbon storage representation, increases resilience and allows functional diversity analysis: a plant-trait vs. PFT-based modeling comparison**

**The inclusion of trait variability enables functional reorganization and decreases impacts of reduced precipitation on carbon storage: a modeling exercise**

**Modeling the impacts of trait variability inclusion on vegetation models in a reduced precipitation scenario: a plant-trait vs. PFT-based comparison**

**Modeled functional diversity role on the impacts of reduced precipitation in Amazon forest carbon storage: comparing a plant-trait vs. a PFT-based approach**

**Comparing a plant-trait vs. a PFT-based modeling approach in a reduced precipitation scenario**

**Functional diversity plays a paramount role on determining impacts on Amazon carbon storage in a reduced precipitation: comparing a plant-trait vs. a PFT-based modeling approach**

**Implication of trait variability on the Amazon carbon storage response to moisture stress: a modeling exercise comparing a plant-trait vs. a PFT-based approach**

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**Introduction**

It is projected, for the 21st-century, that Amazon forest will experience more frequent and more extreme moisture stress (Duffy, Brando, Asner, & Field, 2015; Esquivel-Muelbert et al., 2017; Hubau et al., 2020; Lewis et al., 2011)⁠, what impact directly forest ability to store carbon (da Costa et al., 2010; Hubau et al., 2020; Phillips et al., 2010)⁠ and induce shifts in different facets of biodiversity such as the functional one - the values, ranges of values and relative abundance of functional traits in a given community or ecological unit (Díaz et al, 2007) - (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Zhang, Niinemets, Sheffield, & Lichstein, 2018)⁠. These type of changes conducted by reduced precipitation has been already observed in Amazon forest through long-term inventory plots (Esquivel-Muelbert et al., 2018, 2017)⁠, and experiments (Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007)⁠, as well as in other tropical forests (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012)⁠. However, the degree and direction (increase or decrease) in which the ecosystem process of carbon storage will be affected remain uncertain (Bonal, Burban, Stahl, Wagner, & Hérault, 2016; Hubau et al., 2020; Yang et al., 2018). In addition, both the role that functional diversity plays on this ecosystem process and the impact of the foreseen reduced precipitation on functional diversity itself and on its different components (richness, divergence and evenness; (Carmona, de Bello, Mason, & Lepš, 2016; Mason, Mouillot, Lee, & Wilson, 2005)⁠) is poorly explored (Esquivel-Muelbert et al., 2017; 2018; Poorter et al., 2015; Sakschewski et al., 2016) and still presents many knowledge gaps (Aguirre-Gutiérrez et al., 2019)⁠.

Vegetation models have been widely used to explore the fate of Amazon forest carbon storage under unprecedent climatic conditions such as reduced precipitation, what provided substantial contribution to our current knowledge of the Amazon forest susceptibility (Díaz & Cabido, 1997; Prentice et al., 2007; Scheiter, Langan, & Higgins, 2013). Nonetheless, their results are still contradictory and divergent (Huntingford et al., 2013; Powell et al., 2013; Rammig et al., 2010), although most of them tend to project a drastic loss in carbon stock (P M Cox, Betts, Jones, Spall, & Totterdell, 2000; Peter M. Cox et al., 2004)⁠, together with a replacement on predominant vegetation type composition on large portions of Amazon forest by a drier-affiliated vegetation such as tropical savanna (Hutyra et al., 2005; Lapola, Oyama, & Nobre, 2009; Salazar, Nobre, & Oyama, 2007).⁠

One of the sources for the uncertainties and divergence the models may relies on the way that the diversity of vegetation is represented in most of these models: they commonly use the concept of plant functional types (PFTs) to represent vegetation, a very small, discrete, and *a priori* defined set of plant types, in which the parameters that represent functional traits responsible for ecophysiological process and the connection with environment (i.e., the responses and effects) are fix in space and time for each PFT (Reu et al., 2014; Scheiter et al., 2013; Verheijen et al., 2015)⁠. This simplification of vegetation diversity seems to overestimate the impacts of environmental changes and might also compromise reliability in current conditions projections (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Sakschewski et al., 2016; Verheijen et al., 2015), once diversity of responses and the possibility for selecting alternative strategies that deal better with the new climatic condition present very limited boundaries (Fyllas et al., 2014; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016))⁠. Hence, an important process that confer resilience to novel and unprecedented climatic conditions, the community functional reorganization (Aguirre-Gutiérrez et al., 2019; Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), is very restricted or even not captured (Sakschewski et al., 2016; Verheijen et al., 2015)⁠. In this type of adjustment one can observe a rearrangement of the community in terms of its traits distribution (e.g., frequency and occurrence) and a selection for an alternative functional structure (e.g., relative dominance), composition and diversity (Enquist et al., 2015; Thompson, Mackey, McNulty, & Mosseler, 2009; Wieczynski et al., 2019) through the selection specific groups of plants with characteristics (functional traits) that confers higher ability to deal with the new environmental conditions (Rowland et al., 2015; Esquivel-Muelbert et al., 2017, Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010)⁠⁠.

Besides, the use of PFTs compromises the representation and analysis of functional diversity and its different main components: richness, divergence and evenness, that respond distinctly to disturbances and that play different roles on plant communities (Mason, Mouillot, Lee, & Wilson, 2005; Song, Wang, Li, & Zhou, 2014)⁠. The rearrangement above cited together with modifications on functional diversity components can in turn implicate in important changes on ecosystem functioning such as the carbon cycle (Madani et al., 2018; Esquivel-Muelbert et al., 2017⁠). It also hampers advancements in the comprehension of the yet unknown effects of climate change in functional diversity and other ecosystem processes driven by or emerging from plant diversity (Díaz & Cabido, 2001; Lavorel & Garnier, 2002)⁠. Accordingly, the incorporation of trait variability on vegetation models becomes essential.

In order to overcome these limitations regarding underrepresentation of functional diversity by using PFTs, the so-called Trait-based vegetation models have been developed (e.g., Fyllas et al., 2014; Joshi et al., 2020; Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Sakschewski et al., 2015; Scheiter, Langan, & Higgins, 2013)⁠ . This modeling approach represent plant types in a less discrete manner by replacing the fixed parameters representing the functional traits in PFTs by variable ones (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013⁠; Reu et al., 2014; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010; Wullschleger et al., 2014)⁠, thus increasing the traits diversity and allowing a more flexible representation of plant functional responses to a given environmental condition (Pavlick et al., 2013; Scheiter et al., 2013)⁠. It timely provides the opportunity for models to look beyond biogeochemical variables (e.g., biomass and productivity) creating potential for exploring a multiplicity of functional ecology-related questions (Sakschewski et al., 2016; Darela-Filho et al., in prep.)⁠; for example, the role of the different components of functional diversity on resilience against environmental changes and also identify and predict the processes that determine community assemblage and structure (Mouillot et al., 2013).

Despite the promising potentiality established for trait-based models to explore this type of question many of them remain under or unexplored by the modeling studies so far (but see Hofhansl, Chacón‐Madrigal, Brännström, Dieckmann, & Franklin, 2021⁠). For example, despite the known importance, few studies have explored how environmental changes impacts the different functional diversity components (Carmona, de Bello, Mason, & Lepš, 2016; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013)⁠. Furthermore, the ability of trait-based models to effectively capture (and improve) the representation of ecological processes that are commonly considered in standard vegetation models such as net primary productivity (NPP) and carbon storage is yet to be assessed, as well as the comparative difference in the plant functional response to environmental changes.

Here, we describe for the first time a new trait-based model, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ). First, we evaluate CAETÊ’s performance in representing vegetation carbon storage and net primary productivity (NPP) for the Amazon region. In order to assess if the inclusion of trait variation improves the representation of these biogeochemical variables we compared two approaches of CAETÊ: one representing vegetation through a small number of PFTs (i.e., low functional diversity) and the other one representing vegetation using variant functional traits (i.e., high functional diversity). Six traits were defined to be fixed (PFT approach) or variant (trait-based approach): carbon allocation and residence time in three plant compartments (leaves, aboveground woody tissues and fine roots). We also applied these two modeling approaches in a scenario of reduced precipitation for the sake of representing moisture deficits predicted to Amazon region. By using this scenario we aimed to evaluate how functional diversity (and its different components) impacts Amazon forest ability to store carbon stocks and also how moisture stress change functional diversity considering richness, evenness and divergence. Then, the following hypothesis were tested:

(H1) Using the trait-based modeling approach we will be better able to detect the preserving carbon stocks in the face of the imposed reduced precipitation, since a model approach with higher variability of traits values and combinations than with the PFT approach would provide better capacity to functionally reorganize the community under the new environmental conditions (Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999)⁠, constituting an ensure in the face of local extinctions of strategies and thus a more resilient ecosystem (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019).

(H2) We hypothesize that functional reorganization in communities, especially considering the trait-based approach, will prioritize, based on optimal partitioning theory (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972)⁠, strategies with higher investment (higher allocation and residence time) in fine roots to increase the acquisition of the most limited resource (water in this case). This prioritization of strategies may be due to the expected environmental filtering of a small subset of functional trait combinations more suitable to cope with the applied precipitation reduction.

(H3) Finally, we expect that selection towards more restrict functional traits values may lead to a scenario of communities with lower functional richness (Cornwell et al., 2006; Funk et al., 2017; Kleidon, Adams, Pavlick, & Reu, 2009; Perronne & Gaba, 2017). This restriction would decrease evenness, as the density of traits values would be less regularly distributed, what also might push the values towards more extreme regions of the functional space, favoring strategies with specialized functional trait values, yielding an increase in divergence (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011)⁠. Together, the decrease in evenness and increase in divergence is supposed to conduce to lower utilization of the functional space (De La Riva et al., 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011)⁠.

**Material and Methods**

*The CAETÊ model: an overview*

Here we present an overview of the CAETÊ but an in-depth description of the model (including all the ecophysiological processes equations) can be found in Appendix A.3. As a trait-based model, CAETÊ focus on representing a higher variability of plant functional traits and, whenever possible, the range of functional diversity found in plant communities. As such, vegetation is represented by a set of functional strategies (hereafter called plant life strategies, PLS), each of which refers to a unique combination of functional traits values. The combination of such trait values describes the ecophysiological behavior of plants and their relationship with the environment. These traits control, for example, the differential acquisition of carbon, light and water, ultimately defining how the strategy copes with the environment and, together with the other PLSs of the community, determine ecosystem functioning (Fig. 1).

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

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

The differential survival and abundance between PLSs are made possible because each functional trait in the model is related to at least one trade-off (cost-benefit relationship) leading to different relative performances and ability to deal with the environment. The trade-offs also prevent the model from creating the so-called “Darwinian demons” (i.e., maximizing all the functions that contribute for fitness; Scheiter et al., 2013)⁠. Since functional traits both respond to and affect ecosystem-level processes (Díaz et al., 2013; Funk et al., 2017; Lavorel & Garnier, 2002)⁠ the varying PLSs ecophysiological performance generates heterogeneous biogeochemical fluxes and stocks and functional diversity through space and time. Such model outputs are aggregated to the grid cell scale according to the modeled abundances of PLSs, which are determined on the basis of the biomass-ratio hypothesis (Grime, 1998; see Supporting Information SI.1.1.a)⁠. The ecophysiological processes linked to each functional trait, its trade-offs, and associated formulations are summarized in Table A.3 and described in Appendix A.3.2.

*Input data*

The following climatic data were used as inputs for the model: air surface temperature, precipitation, shortwave radiation, relative humidity and atmospheric CO2 concentration. The first four variables were obtained from mean monthly data for the period between 1980 to 2010. which are available in the Inter-Sectoral Impact Model Intercomparison Project 2 (ISI-MIP2; Warszawski et al., 2014)⁠. Atmospheric CO2 concentration was obtained from the National Oceanic and Atmospheric Administration platform (http://co2now.org/images/stories/data/co2-mlo-monthly-noaa-esrl.pdf), using the mean value (considering all the years) of [CO2] for the same period of the others climatic data.

*Simulations setup*

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

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

We set six functional traits to be variable between PLSs/PFTs; since our focus of analysis here is on the process of carbon storage three of them regard the percentage of the carbon distributed to different plant compartments (i.e. carbon allocation to leaves, roots and aboveground woody tissues (hereafter ABGW)) and the other three traits represent carbon residence time - how long the carbon remains - in each one of the plant compartments above cited. Together, these functional traits ultimately define the amount of carbon in each plant tissue of a PLS or PFT at each time step, and are of primary importance for determining absorption and storage of carbon in the study system (Chambers, Fisher, Hall, Norby, & Wofsy, 2012; Fatichi & Leuzinger, 2013; Malhi, 2012; Norby et al., 2005)⁠.

Three tropical PFTs were defined in the PFTA to describe the vegetation encompassing the majority of PFTs previously used in standard DGVMs. The parameters that represent the functional traits used for this study were *a priori* defined following values already used in previous DGVMs (Table SI.1). In the trait-based model approach, the initial range of values for each functional trait considered as variable (from where some of them will be sampled to create the hypervolume) are indicated in Table SI.2. CAETÊ works at a spatial resolution of 0.5º x 0.5º and is coded mainly in Fortran 90 with some modules written in Python.

*CAETÊ performance evaluation*

A first simulation run was designed to evaluate and compare the performance of the two CAETÊ approaches in representing the spatial distribution of vegetation carbon storage and NPP in the Amazon region. For this we compared our model results with reference data obtained from literature and databases through linear regression and by computing the absolute difference between values simulated by CAETÊ and those reference ones for each grid cell. For carbon storage we used data from Baccini et al. (2012) and Saatchi et al. (2011), and for NPP we used data from the MODIS NPP Project (MOD17A3; data available at http://www.ntsg.umt.edu/project/mod17).

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

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

*Representation of functional diversity and composition*

The value of each of the six variant functional traits in each grid cell is represented by a mean value that is estimated according to the relative abundances of PFT/PLSs (see Appendix A.3.1) using the Community Weighted Mean (CWM) metric (Díaz et al., 2007; Grime, 1998)⁠. Here we focused on a large-scale analysis of functional diversity for the whole Amazon basin, in that sense the trait values distribution used to evaluate functional diversity corresponds to the values obtained for all the grid cells; hence the trait variation within a grid cell is not considered.

Following the definitions and methods by Carmona et al. (2016) we considered that single-trait functional diversity can be decomposed into three components: (i) functional richness: the portion of the total functional trait space, i.e, the total range of values for a specific functional trait, that is occupied in an ecological unit derived from the variance of trait values of all the considered organisms (PFT/PLSs in our case); (ii) functional evenness: the regularity of the density distribution of the PLSs’ or PFTs’ trait values in the functional trait space; (iii) functional divergence: the degree to which the abundance of PFT/PLSs’ trait values are distributed towards the extremes of their functional trait space. Carmona’s method uses probability density distributions for the calculation of the components, the so-called TPDs (trait probability distributions). A detailed description of the method and of the R library can be found at <https://CRAN.R-project.org/package=TPD>.

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

For multi-trait functional diversity, we used a hypervolume metric following Blonder et al. (2014; <https://CRAN.R-project.org/package=hypervolume>), which combine the distribution of *n* trait values to calculate functional diversity components (Barros et al., 2016; Blonder et al., 2018)⁠, as, for example, the volume size, that indicates how much of the possible functional space an ecological unit occupies (i.e., the variance of values; Barros et al., 2016), that can be interpreted as functional richness. Also, the distribution of values within the hypervolume informs, together with the centroid (that indicates the mean values), about system functional composition.

As recommended by Barros et al. (2016), before construct the hypervolumes, we performed a principal component analysis (PCA) with a centered and scaled method (for more details see S.M. XXXX and Fig. SI.2). This previous step was necessary because our traits showed correlation and also exceeded the maximum number of variables for constructing the hypervolume in the used metric (Blonder et al., 2014)⁠. Then, the PCA allowed the delineation of the hypervolume using the factor scores of the chosen PC’s (SM XXX) and, additionally, indicates the trade-offs that emerge from the model results.

*Reduced precipitation experiment*

In order to explore the potential effects of functional diversity on the Amazon’s carbon storage in a scenario with reduced precipitation, as well as the response of functional diversity *per se,* we applied a homogeneous reduction of 50% on precipitation for the whole studied area. With homogeneous we mean that the reduced precipitation was applied for the whole period of the study and for all the grid cells equally. Then, specifically, in this modeling experiment we were interested in testing if a plant community with higher functional diversity (trait-based approach) responded differently to the climate in its ability to store and partition carbon compared to a community with lower functional diversity (PFT approach).

With this experiment we did not intend to make reliable predictions regarding the foreseen drought for the region, since we are aware that the tendency for drought is not homogeneous along the basin neither through time. Hence, this applied scenario in this study lends itself as proof of concept by showing: (i) the feasibility of trait-based models in being used to explore the effects of environmental changes in ecosystem functioning and in functional diversity (taking into account its different facets); (ii) that models based in PFTs to represent vegetation may overestimate the effects of these changes given the underrepresentation of functional diversity; and (iii) that the functional diversity of an ecosystem is tightly related to ecosystem processes and functioning, playing a vital role in its responses to environmental changes.

For the analysis related to carbon storage we compared the degree of change in carbon stock either considering the whole plant or the compartments separately for both modeling approaches. In the single-trait analysis, we compared the TPDs generated by the two climatic scenarios for each of the six traits. For this, the dissimilarities between the two TPDs (regular climate and reduced precipitation) were computed by calculating the degree of overlap between the two distributions (dissimilarity index that can vary from 0 – completely functionally similar - to 1 – completely functionally different; Carmona, de Bello, Mason, & Lepš, 2016). This index shows if functional structure of the community was significantly modified by the new climate scenario (Carmona, de Bello, Mason, & Lepš, 2019)⁠⁠. We also compared how the three facets of functional diversity aforementioned changed after the drought.

For the multi-trait analysis four hypervolumes were constructed and compared using the factor scores of the PCA (see SMXXX): one for each model approach and climatic scenario. After, we compared the changes in hypervolumes driven by reduced precipitation in terms of its sizes (richness), the distances between the centroids [i.e., central tendency, that represents the change in mean values and in the occupied region of trait space (Boersma et al., 2016)⁠], and finally, the degree of overlap through Jaccard similarity index that ranges from 0 (completely dissimilar) to 1 (completely similar). These three metrics together indicate the magnitude of change in functional diversity and composition in response to the applied scenarios considering the two applied modeling approaches.

**Results**

*Evaluating CAETÊ performance*

Figure 2 (a, b and d, e) shows the differences between simulated aboveground carbon storage and two reference maps, Saatchi et al., (2011) and Baccini et al. (2012), considering two different CAETÊ approaches (PFTA and TBA). We also show in Figure 2 (c, f) a direct comparison between the simulated and the reference values for each grid-cell.

Both CAETÊ approaches show some over or underestimated values for carbon stocks when compared to the reference data, which can be seen both by the map differences and in the direct comparison. PFTA tends to overestimate carbon stock in most of the Amazon basin, mainly in the central region and at the basin edges, hence, in general, PFTA shows low agreement and large discrepancies in the range of values relatively to the data used as reference. On the other hand, TBA presents better agreement with references, matching the observed values reasonably well, presenting more areas with no differences between simulated and reference values (white cells in Fig. 2b and e) as well as higher number of points closer to the 1:1 line (Fig. 2c and f). However, where TBA simulation doesn't totally match with the estimations by Saatchi et al., (2011) and Baccini et al., (2012) it tends to subestimate mean carbon values, for example in the east and southwest of the basin. The same way as for PFTA, TBA overestimates carbon stocks mainly at the edges of the studied region.

Within the studied region, the model CAETÊ simulated a total aboveground carbon stock of 127.89 and 85.99 PgC for PFTA and TBA, respectively; while Baccini et al. (2012) estimated 80.23 PgC and Saatchi et al. (2011) 71.67 PgC; it demonstrates that TBA also better agree with references regarding carbon stored in Amazon basin.

The comparison with remote sensing NPP estimation (MODIS) reveals that TBA is able to capture the broad spatial patterns of NPP reasonably well (Fig. SI.3b), despite of an underestimation at Andean region and a small overestimation in the northwest/central basin region. On the other hand, PFTA presents a widespread and prominent overestimation for this variable (Fig. SI.3a), except for the underestimation, likewise TBA, at the Andean region. The higher agreement of TBA with MODIS data when compared to PFTA can also be seen in Figure SI.4c, which shows a grid-by-grid cell performance comparison between CAETÊ and MODIS.

The CAETÊ model simulated a total annual NPP of 122.28 PgCyr⁻¹ for Amazon basin when considering PFTA and of 76.05 PgCyr⁻¹ when considering TBA. MODIS estimations reach a value of 74.61 PgCyr⁻¹ for the same variable. Thus, the total NPP value simulated by CAETÊ in its trait-based version (TBA) is much closer to the value estimated by MODIS, which, together with the comparisons related to the above-ground carbon stock, evidences the ability of the TBA approach to better represent key biogeochemical variables.

Direct comparisons between simulated values and *in situ* measurements of aboveground carbon storage, total carbon storage and NPP showed similar patterns to previous comparisons, i.e, overestimation of all variables by PFTA and underestimation by TBA (Fig. SI.4).

*Reduced precipitation impacts on carbon storage and partitioning: trait-based vs. PFT approach*

As expected, the 50% reduction of precipitation caused a widespread depletion of carbon stocks along the basin both for the high and low degrees of functional diversity employed in the model, including grid cells that presented a total carbon loss (Fig. 3a and b). However, in line with the hypothesis H1 the spatial pattern of carbon loss driven by the imposed moisture deficit differed between the trait-based and PFT approaches: TBA was able to maintain carbon stocks in some areas where in PFTA carbon stocks were completely lost, that is, none PFT survived in those grid cells. This was more evident in central Amazon and in naturally drier areas, such as the transition between the Amazon forest and the savannah (*cerrado*) in the southeast region. It is noteworthy also that the loss of carbon in TBA was more gradual, i.e., there is a smoother gradient between a grid cell value and its neighboring cells, and also across different basin regions. On the other hand, in the PFTA the carbon loss was more abrupt both between neighboring cells and along the regions of the basin.

Supporting our hypothesis H2 specific plant compartments have shown different patterns of changes when comparing the two approaches (Fig. 3c and 3d for fine roots and Fig. SI.5a and b for leaves and Fig. SI.5c and d). None of the compartments has shown, for any area, an increase in carbon stock with precipitation reduction, except for the fine roots compartment in TBA (blue areas in Fig. 3d). It was more evident in the transitions from humid and evergreen forest to the Brazilian savannahs (*cerrado*) and also in the northwest of the basin (naturally drier sites). The increase in fine roots investment also indicated change in carbon partitioning (root:shoot relation) towards higher belowground investment in TBA but lower belowground investment in PFTA: we found an average increase of 74.74% on this variable for TBA while for PFTA an average decrease of 7.73% was observed.

An interesting and important result with the experiment scenario was the unexpected higher total carbon storage in PFTA when compared to TBA in grid cells where both approaches were able to maintain at least a minimum carbon stock (Fig. 3a and b). It goes against our hypothesis H1 in which we predicted higher carbon stocks maintenance for TBA.

*Effects of moisture stress on functional composition*

In our hypothesis H2 we predicted a functional reorganization in communities driven by the reduced precipitation. As we expected, the applied moisture stress scenario caused a modification in the density distribution of the six variant functional traits both for PFTA and for TBA (Fig. 4). For all the traits, the shape of the curves changed considerably, with dissimilarity index close to 1 (Table XXX), which indicates that they became functionally different with the new climatic condition. A clear change in the pattern of traits distribution was observed: dominance reduction (decrease in the curves peaks) of a previously restricted range of values, and density increase of other trait values that were previously rare (very low density), or absent, enabling their co-occurrence in the trait space (Fig. 4). The occurrence of a small subset of trait combinations with the reduced precipitation due to the stronger environmental filtering was not so evident, as expected by our hypothesis H2.

Despite both approaches have shown functional reorganization the degree of change was quite different between them: when considering traits separately, the PFTA showed a trimodal distribution, with three clear and discrete peaks along the trait space when the precipitation is reduced, while in TBA the distribution showed a higher diversity of values that had their density increased, resulting in a much more diffuse distribution within the functional space. This pattern can also be seen when considering all traits together through the hypervolumes: for the PFTA it is possible to observe three clear data grouping under drought (Fig. 5a), and a much less discretized data distribution from the TBA (Fig. 5b).

Also, corroborating with our conjectures based on optimal partitioning theory (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972)*⁠,* TBA showed an increase in density towards higher values of carbon allocation in fine roots and towards lower values of carbon allocation in leaves and, especially, in ABGW (Fig. 3a-c), and an increase in residence time for leaves and for fine roots but a decrease for ABGW (Fig. g-i). Despite our results showing a change in the values’ occurrence patterns along the trait space for PFTA in the applied low precipitation scenario, the magnitude of this change in values throughout the functional space is much lower than for TBA, i.e., with almost no alteration in the range of values (see x axis in Fig. 3). These differences support our assumptions (H1) that a trait-based model show a higher capacity to functionally reorganize the community under the changes in environmental conditions.

*Reduced precipitation impacts on functional diversity facets*

The above-cited changes drove alterations in the three facets of functional diversity within the two employed modeling approaches (Fig. 6; Table XX). Contrasting to our predictions in H3 that the applied precipitation reduction would decrease the richness of trait variation in the communities, we found an increase in functional richness for all traits in both approaches (Fig. 6a), except for residence time in ABGW for the PFTA. Also, the percentage of change in this facet was much higher in TBA, for example, while the TBA presented an increase of 15.15% in richness for leaf allocation, PFTA showed an increase of only 0.47% for the same variable. For all the traits in the TBA, we observed an increase superior to 100% for functional evenness facet, while in the PFTA, the result was the opposite: traits showed a decrease in this functional diversity component, except for allocation and residence time in AGBW (Fig. 6b). The evenness result for TBA differ from our assumptions pointed out in H3 that this functional diversity facet would decrease because of the expected selection of a narrow range of trait values. In line with richness, the change in evenness for the PFTA traits was in a much lower degree of change (74% maximum) when compared to TBA. While leaf allocation displayed an increase of more than 200% for functional divergence, the other TBA traits presented reduction in this variable, mostly in disagreement to our H3 (Fig. 6c). However, in accordance with our third hypothesis, divergence in the PFTA presented an increase in its functional traits, with the exception of leaf allocation and residence time in ABGW (Fig. 6c). Likewise, the other functional diversity facets, the changes observed for PFTA was in a smaller magnitude than for TBA.

Also, with the applied change in precipitation, the hypervolumes for TBA and PFTA showed a pronounced change (Fig. 5; see Movie SI.1 for a 3D animated representation): under natural climatic conditions the size of the volume that the data occupy was equal to 1.711 and 0.007 for TBA and PFTA, respectively; while under reduced precipitation the volume size increased for both approaches: 47.837 for the former and 0.755 for the latter. This result reinforces the refutation of our second hypothesis. The overlap degree between hypervolumes (before and after the drought scenario) yielded a value of 0.038 for the TBA and of 0.009 for the PFTA, indicating almost no similarity between the hypervolumes. Finally, the distance between the centroids of the two hypervolumes after imposing a climatic change indicated a change in the mean values: the centroid distance for the TBA was 5.25 and 0.937 for the PFTA, that is, the mean values were modified in a higher magnitude for the former approach with the applied reduced precipitation.

**Discussion**

Briefly, our results showed: (i) TBA presented better performance in representing carbon stocks and NPP against references; (ii) moisture stress induced carbon losses more smoothly in the TBA throughout the studied area, which also occupied areas where PFTA could not establish; (iii) all the plant compartments showed a reduction in storing carbon, except for fine roots in TBA, that presented an increase of investment in this tissue to deal with the lower water availability; (iv) this increase in fine roots investment for TBA can be attributed to the higher capacity of this modeling approach to functionally reorganize its community composition; (v) both modeling approaches presented changes on the three facets of functional diversity, however the magnitude of the change was much higher in TBA because of available trait variability.

*Evaluating CAETÊ performance*

Trait-based models developers have argued that the inclusion of trait variation is able not only to represent biogeochemical cycles but to improve accuracy when compared to models based on PFTs. Theoretically, this improvement emerges from the fact that by representing vegetation with only few PFTs and fix values representing their functional traits widely contrast with the massive trait variation observed in nature, especially in hyperdiverse ecosystems such as Amazon, and as a consequence do not account for the responses to local environmental heterogeneity and constraints (Ackerly and Cornwell, 2007; Freschet et al., 2011; Westoby et al., 2002, Verheijen et al., 2013). In order to test these statements and contribute to the development of trait-based models we here implemented trait variation in a version (TBA) of the vegetation model CAETÊ and compared it with a version using a PFT approach (PFTA).

Our results show that the inclusion of trait variation in vegetation models in fact plays a paramount role in predicting vegetation carbon cycle: the TBA was not only able to represent NPP and carbon storage reasonably well when compared to references both considering geographical distribution and total values, but also showed higher agreement when contrasted to PFTA (Fig. XXX). The accuracy improvement in represent biogeochemical variables by adding trait variability was already observed in other modeling exercises (Fyllas et al., 2014; Sakschewski et al., 2015; L. M. Verheijen et al., 2013; Lieneke M. Verheijen et al., 2015). We attribute this improvement to trait variability inclusion, since it confers a higher diversity of responses in communities to environmental filtering derived from climatic heterogeneity allowing a more realistically simulation of the community assembly (Keddy, 1992)⁠ and, as a consequence of the biogeochemical cycles (Sakschewski et al., 2015; L. M. Verheijen et al., 2013)⁠.

The PFTA presented a generalized overestimation of aboveground carbon storage and NPP (Fig. XX and XX) when contrasted to reference maps that is derived from the fact the PFTs (chosen by previous PFTs implemented in DGVMs) are already parameterized to present a high performance (or optimal trait combination) in the climatic envelope found in regions with predominance with tropical forests (Scheiter, Langan, & Higgins, 2013; L. M. Verheijen et al., 2013)⁠. It allows a high survivorship of individuals with high carbon storage, what is especially important in simulation with CAETÊ since our scaling for the grid-cell is weighted by the biomass of PFTs present in this cell (see XXX).

PFTA and TBA presented some common mismatch with the reference maps regarding carbon storage. Both approaches present an overestimation of values at the edges of Amazon basin when compared to the maps estimated by Saatchi et al. (2011) and Baccini et al. (2012). This is linked to the fact that these regions that are known to be heavily deforested, but the model CAETÊ still do not incorporate human land use nor fire for determining vegetation distribution. Also, either PFTA and TBA present a tendency for overestimating carbon storage and NPP in central/northwest of Amazon basin. It might be linked to forcing linked to ecological processes (such as competition and demography) and edaphic features (such as available nutrients, especially nitrogen and phosphorus) that are still not represented in CAETÊ.

Our findings, besides emphasizing the importance for incorporating trait variability in represent vegetation and biogeochemical cycles in current climate also bases the idea that it probably also allows more reliable projections in unknown and unprecedented climates.

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

As expected, the 50% reduction in precipitation caused a pervasive decrease in the basin carbon stock for both modeling approaches, concentrated mainly on the Amazon basin edges and other naturally drier regions (Fig. 2a and 2b). This massive decrease of Amazon forest ability to store carbon in moisture stress scenarios is in agreement with experimental (da Costa et al., 2010; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007)⁠⁠, observational (Brienen, Phillips, Feldpausch, & et al., 2015; Enquist & Enquist, 2011; Phillips et al., 2009, 2010)⁠⁠ and previous modeling studies (Lapola, Oyama, & Nobre, 2009; Powell et al., 2013; Rammig et al., 2010)⁠. In our model, this decrease is a result of the strengthened soil moisture stress that reduces photosynthetic rates and net primary productivity, meaning that the carbon available to be invested in plant compartments is reduced, a mechanism also known as carbon starvation (Doughty et al., 2015; Rowland et al., 2015)⁠.

Despite the general decrease in carbon stocks, we found important differences between PFTA and TBA regarding the geographical pattern of carbon loss: firstly, it is noteworthy that for TBA it occurred in a much smoother gradient between a grid cell value and its neighboring cells, and also across different basin regions; and second, TBA was able to maintain carbon stocks in some areas where in PFTA carbon stocks were completely lost, that is, none PFT was able to establish. This was more evident in naturally drier areas, such as the transition between the Amazon forest and the savannah (*cerrado*) and central Amazon, that, in general, were the more affected regions. It corroborates with our H1 and with previous literature in which it is widely accepted that a more diverse (both taxonomically and functionally speaking) ecosystem tends to be less impacted by environmental changes (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019)⁠.

This connection between functional diversity and resilience to environmental changes emerges from the fact that higher variability of traits (and plant strategies) also provides higher diversity of responses under new conditions, so that the community can restructure and maintain the ecosystem processes or decrease the impact of change, showing, hence, higher resilience (Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016;Mori et al., 2013; Yachi & Loreau, 1999)⁠. Previous theoretical, experimental and modeling literature have already shown that environmental change is able to cause a modification on functional structure (Enquist & Enquist, 2011; Hillebrand, Bennett, & Cadotte, 2008; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011)⁠, dominance (Hillebrand et al., 2008; Schmitt et al., 2019; Valencia et al., 2015)⁠, composition (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007)⁠ and diversity components (Hillebrand et al., 2008; Zhang, Chen, & Reich, 2012)⁠. In fact, our results showed that the modeling approach with higher diversity (TBA) presented a significant functional community reorganization of Amazon forest in terms of composition, dominance relationship, functional richness, evenness and divergence with the applied precipitation reduction scenario (Fig. 3, Fig 4 and fig. Com os plots separados).

Functional reorganization can occur through a compensatory dynamic process so called as “functional density compensation” when the composition (that is, the occurrence or abundance of trait values) of a community adjust to the new conditions enabling types of plants - or trait combinations, in our case - that previously exerted a less relevant functional role (i.e. low density) to increase their dominance and vice-versa (Gonzalez & Loreau, 2009; Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016), then, changing the way that community occupy the functional space⁠. Such a functional density compensation followed by functional reorganization and its restriction by traits variability was well captured in our modeling results: reduced precipitation led to an expressive wider range of traits values in functional space for all the considered traits for TBA, while PFTA presented a restricted probability of the occurrence of new trait values, presenting trimodal curves with moisture stress, product of *a priori* defined trait values. This was also observed in the multi-trait analysis of functional diversity: the wider occupation of the functional space with the reduced precipitation was much stronger in the TBA when compared to the PFTA, as well as the centroid distance before and after disturbance.

The capacity to functionally reorganize enabled a paramount change on TBA that corroborates with our H2: the increase in the abundance of traits with higher values of allocation and residence time for fine roots (Fig. XXX) led to higher investment in this plant compartment to the detriment of investment in leaves and ABGW (Fig. XXX), a result imposed by the CAETÊ trade-offs. It reflected in carbon partitioning for TBA, that is, a bigger root:shoot when compared to the regular climate condition (Fig. XX). The higher investment in fine roots increased the uptake of water, which makes the community better able to deal with drought and maintain carbon stocks or reduce the degree of loss. These results corroborate with the well known effect of climatic change, such as drought, in inducing changes on C partitioning patterns (Doughty et al., 2014; Kannenberg et al., 2019)⁠ including a prioritization of root investment at the expense of other tissues (Doughty et al., 2014; Phillips et al., 2016; Rowland et al., 2014)⁠. On the other hand, given the limited trait variability, PFTA did not show this plasticity in carbon partitioning, avoiding its PFTs to establish in some grid cells, especially those that naturally show lower levels of precipitation (Fig. XXX).

Understanding the shift in carbon partitioning due to climate is of primary relevance for the future of Amazon carbon stocks (Doughty et al., 2015; Friedlingstein et al., 2006)⁠ and is especially important if the carbon is allocated towards pools with shorter turnover, such as fine roots or even root exudates (Jiang et al., 2020)⁠, that contribute to a lesser extent to total carbon storage comparatively with other pools such as wood tissues (Chave et al., 2009; De Kauwe et al., 2014; Kannenberg et al., 2019; Luo, 2003)⁠. Our modeling exercise was able to capture this process: the reduce moisture triggered an increase in investment in fine roots in the TBA that provided greater resistance to drought, preventing the total loss of carbon in several grid-cells, and also caused a lower carbon storage in other tissues, mainly on ABGW and led to a relative lower carbon storage in some locations when compared to the PFTA. In that sense, if the ability to store carbon is used as the only proxy for ecosystem resilience, as is commonly used, e.g., Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016, it may result in limited interpretations about the response of tropical forests to climate change. Also, our results showed that the approach used in vegetation models that seek to represent the impacts of environmental change in ecosystems indeed matters: the use of a small set of PFTs with fixed parameters to represent vegetation can overestimate the impacts of these changes and impose limitation on looking into processes such as the change in communities functional structure.

*Community reorganization change functional diversity facets*

Few studies have explored how moisture stress impacts the different functional diversity components (but see Hofhansl, Chacón‐Madrigal, Brännström, Dieckmann, & Franklin, 2021)⁠ despite the known importance of them for ecosystem functioning and resilience (Carmona et al., 2016)⁠. Here we explored, for the first time, the impact of reduced precipitation on Amazon functional diversity considering its three primary components: richness, evenness and divergence, and also examined functional diversity considering all the six chosen functional traits together.

The functional reorganization found in our results modified the three evaluated functional diversity facets both for single and multi-trait analysis, in accordance with hypothesis H3. But, as expected, because of the lower ability of PFTA to reorganize its functional diversity, alterations considering this approach were in a much lower degree when compared to TBA (Fig. XX). One of the main mechanisms that underly change on diversity facets in communities is the differential occupation of functional space driven by a disturbance (Boersma et al., 2016)⁠, such as moisture stress. The occupancy of distinct regions in functional space after disturbance can be caused by a change on the central tendency, occurrence, abundance and dominance relationship of trait values (Boersma et al., 2016; Carmona, de Bello, Mason, & Lepš, 2019)⁠, as we observed in our results (Fig. XXXX).

In H3 we hypothesized that the stronger environmental filtering imposed by reduced precipitation would restrict functional traits values and combinations for those that could deal with the new conditions, leading to a smaller occupation of functional space, that is, a decrease in richness. This hypothesis has been supported for a variety of studies (Boersma et al., 2016; Mason, Mouillot, Lee, & Wilson, 2005; Swenson et al., 2012; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010)⁠. Nonetheless our results displayed a completely opposite tendency: the reduced precipitation increased the occupancy of functional space and richness in a great order of magnitude, both when looking into traits separately (Fig. XXX and Fig XX) and traits together (Fig. XXX). It might be explained by the paramount role that decrease in dominance exerted after the new precipitation scenario was applied, since it allowed new combinations of traits to establish or to increase their occurrence. These outcomes aggregate evidences that, in some cases, functional richness can increase in disturbance scenarios if the environmental change affects mainly the dominant strategies or trait values (Boersma et al., 2016; Funk et al., 2017; Mouillot et al., 2013).⁠

We also supposed in H3 that a more restrict selection of trait values would decrease evenness as the density of traits values would be less regularly distributed. But, also contrary to our expectations, the evenness exhibited an increase for all considered traits for the TBA. On the other hand, the PFTA showed a decrease in this functional diversity component for the majority of traits. The evenness increase in TBA is tightly related to the observed decrease of dominance and increase of abundance of trait values that were very rare before the disturbance. The decrease in evenness for PFT approach can be explained by the fact that the reduced precipitation decreased the dominance of a very restricted range of trait values (dominance of one PFT) and allowed the occurrence of the other 2 PFTs. Since the difference between the PFTs is very discretized, the occurrence of trait values ended up concentrated in three peaks of density hence turning the distribution less even. Evenness can also be interpreted as an evidence of the effectiveness in using the functional niche space⁠: the higher the evenness, the higher the utilization of the total functional space (De La Riva et al., 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011)⁠. Therefore, our results indicate that a change in the environment can force the community to better occupy the functional niche space, contrary to our expectations in H3, providing, in that matter, lower sensibility to environmental changes, if it presents a sufficient variability in its trait values, as we observed for the TBA.

Modifications in functional divergence indicates changes in the total abundance that is supported in a community by the plant life strategies with the most extreme functional traits, that is, that occupy the extremes of functional space (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Villéger, Mason, & Mouillot, 2008)⁠. In that sense, a higher divergence means that the community is supported by more specialist strategies (Mouillot et al., 2013; Villéger, Miranda, Hernández, & Mouillot, 2010)⁠. Since we expected a more restrict occurrence of trait values, we also assumed that the occupation would be towards the extremities of functional space (H3), i.e., a higher degree of specialization in terms of trait values to deal with the imposed environmental change. However, contrary to our expectations the TBA presented a general decrease in divergence (Fig. XX) . In TBA approach the most plausible cause for the decrease in divergence seems to be the expressive decrease in abundance of dominant trait values, which tended to concentrate at the extremes of functional spaces; as a consequence, other trait values that were not so expressive before became significant for the community. Based on an empirical evidence by analyzing a disturbance gradient, Mouillot et al. (2013) also found a decrease in divergence the greater the disturbance, which was attributed to a declining abundance of the specialist species that were the most impacted by the disturbance. In addition, this decrease in divergence can be an evidence that the frequency distribution of trait values in the functional niche space maximizes the total community variation in functional characters (Mason et al., 2005). On the other hand, PFTA showed a general increase in divergence (Fig. XX), that may be only a product of the emergence of the three peaks on traits distribution previously determined; for this approach an improvement in the occupation of functional space (low divergence) is impossible considering its very low diversity of trait values available, what can confer higher sensibility to disturbances (Villéger et al., 2010).

**Caveats**

Like in all modeling studies, it is necessary to take into account the caveats related to model simplifications and assumptions in order to better understand the results and identify possible next steps for model improvements or even for new studies. The first, and probably the most important, is based on the fact that the model does not present a plant hydraulics module yet, then we were not able to use direct variant traits that are connected to moisture stress impacts on essential plant hydraulics features, such as vulnerability to cavitation and embolism. This representation is crucial considering that several studies have claimed that the decrease in carbon storage due to moisture stress is not, necessarily, linked to a decrease in carbon availability (i.e., carbon starvation) but much more related to hydraulic failure (Eller et al., 2018; Doughty et al., 2015; Phillips et al., 2010; Rowland et al., 2015). Also, our model does not consider the effects of biotic interaction such as mechanistic competition and facilitation, what seems to play a vital role in determining community assembly and ecosystem functioning (Mori et al., 2013). Also, nutrient cycling representation on vegetation models, mainly nitrogen and phosphorus, have been shown to be essential for a reliable representation of carbon storage along Amazon basin. In that sense, we strongly recommend that further studies using vegetation models, including CAETÊ, that aim to understand the impacts of moisture stress on Amazon forest carbon stock, should consider plant hydraulics traits, biotic interactions and nutrient cycling. All these features are being implemented in CAETÊ.

Regarding functional diversity analysis, for this study, we considered the whole Amazon basin as a single ecological unit, which may lead to an oversimplification of diversity within the basin. In order to avoid it, 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 look into 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.

Finally, the reduced precipitation scenario applied in this work was essential to test the posed hypotheses, however, it does not reflect a realistic scenario in which the foreseen drought for the studied region is not homogeneous in space, in time and in magnitude. Hence, further studies may consider using more reliable scenarios for drought patterns and also consider other climatic variables such as temperature and CO2 concentration, also predicted to suffer changes in the next early decades.

**Conclusions**

The quest to reach a more reliable representation of functional diversity in vegetation models and, supposedly, as a consequence, a higher confidence in its projections lead to the development of trait-based models. However, few studies so far have investigated in depth if the inclusion of trait variability in fact improves the representation of ecosystem properties such as NPP and biomass, an important refinement that could improve reliability of projections with future climatology. Additionally, trait-based models also provide an unique opportunity to promote insights in active ecology areas of debate, such as the role of functional diversity in ecosystem response to projected disturbances like climate change, and how functional diversity itself responds to these disturbances. However, this potentiality of trait-based models has yet to be fully accessed and can be considered a far-reaching achievement especially to community ecology.

Here, in this modeling exercise, we compared for the first time how the use of a PFT approach (widely used by vegetation models) differs from a trait-based approach in terms of current representation of carbon storage and NPP; the impacts of a reduced precipitation scenario on how these two approaches simulate carbon storage and functional diversity and how changes on functional diversity components are connected to carbon storage responses.

In this study, the use of a PFT based approach and a trait-based approach applied to the same model, constituted a proof of concept to strengthens the significance of incorporating functional diversity in vegetation models. For example, our results evidenced that the inclusion of trait variability can improve accuracy in representing biogeochemical variables and also show that trait-based models, such as CAETÊ, are important tools to investigate community ecology mechanisms and processes that link biodiversity (mainly functional diversity) and ecosystem functioning. For instance, we found, consistent with expectations, that more diverse communities (trait-based approach) could deal better with environmental changes since it provided a higher range of responses, which enabled a community functional reorganization that could buffer, by maintaining or diminishing, the impacts of disturbances in ecosystem properties. On the other hand, because of its limited capacity to change community functional structure, the use of PFTs may overestimate the impacts of environmental changes.

Besides that, our trait-based framework showed to be a first step into the study of the different components of functional diversity (richness, evenness and divergence) against climate change and its connection with ecosystem functioning. As an example, we found, unexpectedly, that a harsher environment can increase functional richness instead of decreasing it, which can be attributed to a reduction in hyperdominance and then creation of new ecological niches for new combinations of functional traits to occupy in the functional space, and as a consequence, a lower sensibility of the ecosystem. This type of result can also be used to understand mechanisms such as community assembly rules.

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

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**Data availability**

Model’s code, as well as the results, can be found at https://github.com/BiancaRius/CAETE\_Rius\_etal\_2021.

**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, 855–865. https://doi.org/10.1111/ele.13243

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, 855–865. https://doi.org/10.1111/ele.13243

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

Barros, F. de V., Bittencourt, P. R. L., Brum, M., Restrepo-Coupe, N., Pereira, L., Teodoro, G. S., … Oliveira, R. S. (2019). Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Niño-induced drought. New Phytologist, 223(3), 1253–1266. https://doi.org/10.1111/nph.15909

Bazzaz, F. A. (1991). Allocation of Resources in Plants : State of the Science and Critical Questions. Plant Resource Allocation. ACADEMIC PRESS. https://doi.org/10.1016/B978-0-12-083490-7.50002-5

Blessing, C. H., Werner, R. A., Siegwolf, R., & Buchmann, N. (2015). Allocation dynamics of recently fixed carbon in beech saplings in response to increased temperatures and drought. Tree Physiology, 35(6), 585–598. https://doi.org/10.1093/treephys/tpv024

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

Blonder, B., Morrow, C. B., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., … Kerkhoff, A. J. (2018). New approaches for delineating n-dimensional hypervolumes. Methods in Ecology and Evolution, 9(2), 305–319. <https://doi.org/10.1111/2041-210X.12865>

Blonder, B. (2019). *hypervolume: High Dimensional Geometry and Set Operations Using KernelDensity Estimation, Support Vector Machines, and Convex Hulls.* R package version 2.0.12. https://CRAN.R-project.org/package=hypervolume

Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., & Camargo, P. (2008). Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: Results of a throughfall reduction experiment. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1498), 1839–1848. https://doi.org/10.1098/rstb.2007.0031

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., & et al. (2015). Long-term decline of the Amazon carbon sink. Nature, 519(7543), 344–348. https://doi.org/10.1038/nature14283

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

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). <https://doi.org/10.1002/ecy.2876>

Carmona, C. P. (2019). *TPD: Methods for Measuring Functional Diversity Based on TraitProbability Density.* R package version 1.1.0. <https://CRAN.R-project.org/package=TPD>

Chambers, J., Fisher, R., Hall, J., Norby, R., & Wofsy, S. (2012). Research Priorities for Tropical Ecosystems Under Climate Change Workshop. Retrieved from http://science.energy.gov/~/media/ber/pdf/NGEE-Tropics\_LR.pdf

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

Christoffersen, B. O., Gloor, M., Fauset, S., Fyllas, N. M., Galbraith, D. R., Baker, T. R., … Meir, P. (2016). Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro). Geoscientific Model Development, 9(11), 4227–4255. https://doi.org/10.5194/gmd-9-4227-2016

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, Pearson, D., Booth, B. B., Friedlingstein, P., Huntingford, C., Jones, C. D., & Luke, C. M. (2013). Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. Nature, 494(7437), 341–344. https://doi.org/http://www.nature.com/nature/journal/v494/n7437/abs/nature11882.html#supplementary-information

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. a., Brovkin, V., … Young-Molling, C. (2001). Global response of terrestrial ecosystem structure and function to CO2 and climate change: Results from six dynamic global vegetation models. Global Change Biology, 7(4), 357–373. https://doi.org/10.1046/j.1365-2486.2001.00383.x

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., Carmona, C. P., Mason, N. W. H., Sebastià, M. T., & Lepš, J. (2013). Which trait dissimilarity for functional diversity: Trait means or trait overlap? Journal of Vegetation Science, 24(5), 807–819. https://doi.org/10.1111/jvs.12008

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

Díaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science, 8, 463–474. https://doi.org/10.1016/0026-0495(83)90194-4

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., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences of the United States of America, 104(52), 20684–20689. https://doi.org/10.1073/pnas.0704716104

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., Amezquita, F. F., Durand, L., Huasco, W. H., … Malhi, Y. (2015). Source and sink carbon dynamics and carbon allocation in the Amazon basin, 1–11. https://doi.org/10.1002/2014GB005028.Received

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., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., … Savage, V. M. (2015). Scaling from Traits to Ecosystems: Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. Advances in Ecological Research (1st ed., Vol. 52). Elsevier Ltd. https://doi.org/10.1016/bs.aecr.2015.02.001

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

Fatichi, S., & Leuzinger, S. (2013). Reconciling observations with modeling: The fate of water and carbon allocation in a mature deciduous forest exposed to elevated CO2. Agricultural and Forest Meteorology, 174–175, 144–157. https://doi.org/10.1016/j.agrformet.2013.02.005

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

Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., … Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. Journal of Ecology, 103(1), 191–201. https://doi.org/10.1111/1365-2745.12346

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

Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, a. K., & Dybzinski, R. (2012). Modeling carbon allocation in trees: A search for principles. Tree Physiology, 32(6), 648–666. https://doi.org/10.1093/treephys/tpr138

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., … Zeng, N. (2006). Climate–Carbon Cycle Feedback Analysis: Results from the C 4 MIP Model Intercomparison. Journal of Climate, 19(14), 3337–3353. https://doi.org/10.1175/JCLI3800.1

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

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., Schnecker, J., Singer, G., & Wanek, W. (2015). New insights into mechanisms driving carbon allocation in tropical forests, 137–146.

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

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

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

Lacointe, A. (2000). Carbon allocation among tree organs: A review of basic processes and representation in functional-structural tree models. Annals of Forest Science, 57(5–6), 521–533. https://doi.org/10.1051/forest:2000139

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B.,  imova, I., … Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. Proceedings of the National Academy of Sciences, 111(38), 13745–13750. https://doi.org/10.1073/pnas.1317722111

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

Lepš, J., de Bello, F., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities : practical considerations matter. Preslia, 78, 481–501.

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

Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. Global Change Biology, 13, 2089–2109. https://doi.org/10.1111/j.1365-2486.2007.01420.x

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

Luo, Y. (2003). Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach. Global Biogeochemical Cycles, 17(1), 1–13. https://doi.org/10.1029/2002GB001923

Malhi, Y. (2012). The productivity, metabolism and carbon cycle of tropical forest vegetation. Journal of Ecology, 100(1), 65–75. https://doi.org/10.1111/j.1365-2745.2011.01916.x

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

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

Nepstad, D. C., Tohver, I. M., Ray, D., Moutinho, P., & Cardinot, G. (2007). MORTALITY OF LARGE TREES AND LIANAS FOLLOWING EXPERIMENTAL DROUGHT IN AN AMAZON FOREST. Ecological Society of America, 88(9), 2259–2269. https://doi.org/10.1038/aps.2015.36

Norby, R. J., Delucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., … Oren, R. (2005). Forest response to elevated CO2 is conserved across a broad range of productivity. Proceedings of the National Academy of Sciences of the United States of America, 102, 18052–18056. https://doi.org/10.1073/pnas.0509478102

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., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., … Torres-Lezama, A. (2009). Drought sensitivity of the amazon rainforest. Science, 323(5919), 1344–1347. https://doi.org/10.1126/science.1164033

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.

Phillips, R. P., Ibáñez, I., D’Orangeville, L., Hanson, P. J., Ryan, M. G., & McDowell, N. G. (2016). A belowground perspective on the drought sensitivity of forests: Towards improved understanding and simulation. Forest Ecology and Management, 380, 309–320. https://doi.org/10.1016/j.foreco.2016.08.043

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

Poorter, Lourens, McDonald, I., Alarcón, A., Fichtler, E., Licona, J. C., Peña-Claros, M., … Sass-Klaassen, U. (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytologist, 185(2), 481–492. https://doi.org/10.1111/j.1469-8137.2009.03092.x

Powell, T. L., Galbraith, D. R., Christoffersen, B. O., Harper, A., Imbuzeiro, H. M. A., Rowland, L., … Moorcroft, P. R. (2013). Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. New Phytologist, 200(2), 350–365. https://doi.org/10.1111/nph.12390

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

Quillet, A., Peng, C., & Garneau, M. (2010). Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. Environmental Reviews, 18(NA), 333–353. <https://doi.org/10.1139/A10-016>

R core team. (2013). *stats: The R Stats Package.* R package version 3.6.2. https://www.rdocumentation.org/packages/stats

Rammig, A., Jupp, T., Thonicke, K., Tietjen, B., Heinke, J., Ostberg, S., … Cox, P. (2010). Estimating the risk of Amazonian forest dieback. New Phytologist, 187(3), 694–706. https://doi.org/10.1111/j.1469-8137.2010.03318.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

Ricotta, C., & Moretti, M. (2011). CWM and Rao’s quadratic diversity: A unified framework for functional ecology. Oecologia, 167(1), 181–188. https://doi.org/10.1007/s00442-011-1965-5

Rowland, L., 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

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, 1–16. https://doi.org/10.1038/nclimate3109

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: learning from community ecology. The New Phytologist, 198(3), 957–969. https://doi.org/10.1111/nph.12210

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

Sevanto, S., & Dickman, L. T. (2015). Where does the carbon go?-Plant carbon allocation under climate change. Tree Physiology, 35(6), 581–584. https://doi.org/10.1093/treephys/tpv059

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

Thompson, I., Mackey, B., McNulty, S., & Mosseler, A. (2009). Forest resilience, biodiversity, and climate change (Vol. 43).

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

Valencia, E., Maestre, F. T., Le Bagousse-Pinguet, Y., Quero, J. L., Tamme, R., Börger, L., … Gross, N. (2015). Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. New Phytologist, 206(2), 660–671. https://doi.org/10.1111/nph.13268

van der Sande, M. T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J., … Peña-Claros, M. (2017). Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. Biotropica, (June). https://doi.org/10.1111/btp.12453

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, 21(8), 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

Warszawski, L., Frieler, K., Huber, V., Piontek, F., Serdeczny, O., & Schewe, J. (2014). The inter-sectoral impact model intercomparison project (ISI-MIP): Project framework. Proceedings of the National Academy of Sciences of the United States of America, 111(9), 3228–3232. https://doi.org/10.1073/pnas.1312330110

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

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science, 10(5), 609–620. https://doi.org/10.2307/3237076

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