Higher functional diversity improves modeling of Amazon forest carbon storage

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ABSTRACT

The impacts of reduced precipitation on plant functional diversity and how its components (richness, evenness, divergence and composition) modulate the Amazon carbon balance remain elusive. We present a novel trait-based approach, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model to investigate the role of plant trait diversity in representing vegetation carbon (C) storage and net primary productivity (NPP) in current climatic conditions. We assess impacts of plant functional diversity on vegetation C storage under low precipitation in the Amazon basin, by employing two approaches (low and high plant trait diversity, respectively): (i) a plant functional type (PFT) approach comprising three PFTs, and (ii) a trait-based approach representing 3000 plant life strategies (PLSs). The PFTs/PLSs are defined by combinations of six traits: C allocation and residence time in leaves, wood, and fine roots. We found that including trait variability improved the model's performance in representing NPP and vegetation C storage in the Amazon. When considering the whole basin, simulated reductions in precipitation caused vegetation C storage loss by ~60% for both model approaches, while the PFT approach simulated a more widespread C loss and abrupt changes in neighboring grid cells. We found that owing to high trait variability in the trait-based approach, the plant community was able to functionally reorganize itself via changes in the relative abundance of different plant life strategies, which therefore resulted in the emergence of previously rare trait combinations in the model simulation. The trait-based approach yielded strategies that invest more heavily in fine roots to deal with limited water availability, which allowed the occupation of grid cells where none of the PFTs were able to establish. The prioritization of root investment at the expense of other tissues in response to drought has been observed in other studies. However, the higher investment in roots also had consequences: it resulted, for the trait-based approach, in a higher root:shoot ratio (a mean increase of 74.74%) leading to a lower vegetation C storage in some grid cells. Our findings highlight that accounting for plant functional diversity is crucial when evaluating the sensitivity of the Amazon forest to climate change, and therefore allow for a more mechanistic understanding of the role of biodiversity for tropical forest ecosystem functioning.

1. Introduction

Climate model projections based on future socioeconomic scenarios indicate that the Amazon forest will experience more frequent and more extreme moisture stress in the 21st century (Lee et al., 2021).

Moisture stress 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

(hereafter C) 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 functional diversity plays in determining vegetation C 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; Reich et al., 2003), functional diversity plays a vital role in determining ecosystem functioning and its responses to environmental changes (Díaz and Cabido, 2001; Song et al., 2014; Cadotte, 2017). Ultimately, functional traits delineate plant communities' responses and effects to biotic and abiotic conditions and also shape ecosystem processes and functions such as vegetation C storage (Lavorel and Garnier, 2002; Funk et al., 2017; Violle et al., 2007). It is widely accepted that more taxonomically and functionally diverse communities are 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 functional strategies provides higher variability of plant functional responses under new environmental conditions (Mori et al., 2013; Yachi and Loreau, 1999), thus maintaining ecosystem functioning by providing a buffer effect against environmental fluctuations (Fauset et al., 2015; Lohbeck et al., 2016; Yachi and 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; Smith et al., 2022).

Accordingly, it has been suggested that environmental fluctuations lead to changes in the abundance of plant strategies that compose the communities and, consequently, changes on how the available functional trait space is occupied, then redefining plant functional diversity components (Boersma et al., 2016; Carmona et al., 2019; de Bello et al., 2021; Enquist et al., 2017). However, there is no consensus under which condition whether environmental changes select traits and lead to homogenization (decrease in functional diversity) or allow multiple functional traits to persist generating diversification (increase in functional diversity; Smith et al., 2022). For example, reduced precipitation was found to exert a strong environmental filter by selecting a subset of functional trait combinations that are more suitable to cope with moisture stress (Mouillot et al., 2013a). In such a scenario, according to the optimal partitioning theory (Cannell and Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972), a common strategy would be to invest more C to fine root production to acquire limiting belowground resources, such as soil water and nutrients required for aboveground plant productivity. Such a selection for more conservative resource-use would restrict the range of functional trait values and thus reduce the functional trait space occupied by the community (lower functional richness; Cornwell et al., 2006; Funk et al., 2017; Kleidon et al., 2009). On the other hand, it has been found that disturbances, especially intermediate disturbances, can trigger an increase in the occupation of the functional trait space (higher functional richness; Herben et al., 2018). In line with the intermediate disturbance hypothesis (Bongers et al., 2009), which predicts that local species diversity is maximized at an intermediate level of disturbance, it has been suggested that also functional diversity should increase via the functional reorganization of the community allowing new ecological strategies to be more abundant in the communities (Smith et al., 2022).

Vegetation models have been widely used to explore the fate of the Amazon forest carbon balance under future potential climatic conditions (Cox et al., 2004; Galbraith et al., 2010; Huntingford et al., 2013; Lapola et al., 2009; Longo et al., 2018; Rammig et al., 2010). Some of these models project a dramatic loss in Amazon forest C stocks due to reduced precipitation (Cox et al., 2000, 2004; Lapola et al., 2009; Oyama and Nobre, 2003). Most model simulations have not reproduced

these patterns afterward but there is ongoing discussion on the likelihood of such projections (Levine et al., 2016; Malhi et al., 2009; Malhi et al., 2018; Lapola et al., 2018). Other models simulate an abrupt replacement of the dominant humid tree cover found in large parts of Amazon forests with more arid-affiliated vegetation under reduced precipitation (Hutyra et al., 2005; Salazar et al., 2007). One of the underlying reasons that models are challenged by simulating unprecedent climatic conditions, is their underrepresentation of plant diversity (Pavlick et al., 2013; Scheiter et al., 2013). Commonly, models represent plant functions based on a very small and discrete set of PFTs (plant functional types) and plant functional traits parameters are previously (*a priori*) defined (Prentice et al., 2007). Consequently, the diversity of plant life strategies, *i.e.,* the combination of traits, found in these model ecosystems is oversimplified and the emergence of alternative trait combinations in response to a changing environmental scenario is strongly limited or is not even captured due to the small number of PFTs that compose the communities (Fyllas et al., 2014; Mori et al., 2013; Sakschewski et al., 2016). As a result, fixed a priori defined parameters commonly lead to an overestimation of the impacts of environmental changes due to abrupt changes in plant performance and establishment success (Berzaghi et al., 2020; Pavlick et al., 2013; Sakschewski et al., 2016; Verheijen et al., 2015) and important mechanisms involved in ecosystem resilience, such as the functional reorganization of the plant community (Enquist and Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), are not represented in such model approaches.

The development of the models with a higher representation of trait variability, so-called trait-based vegetation models (*e.g.,* Fyllas et al., 2014; Joshi et al., 2020, 2022; Pavlick et al., 2013; Sakschewski et al., 2015; Scheiter et al., 2013; Schmitt et al., 2019) is an attempt to overcome these limitations of underrepresenting functional diversity with PFTs. Such a modeling approach allows replacing the small number of PFTs with a more realistic representation of functional diversity, and thus increasing the representation of possible functional traits combinations by several orders of magnitude (Pavlick et al., 2013; Reu et al., 2014; Webb et al., 2010; Wullschleger et al., 2014). This provides the opportunity to explore multiple aspects of plant ecology and community composition in combination with biogeochemical fluxes and pools (Berzaghi et al., 2020; Sakschewski et al., 2016; Zakharova et al., 2019). For example, trait-based vegetation models are able to explore the role of different components of plant functional diversity on ecosystem functioning, the processes that determine community assembly and structure, and how these interact with environmental changes (Fisher et al., 2018; Mason et al., 2005; Mouillot et al., 2013b; Song et al., 2014).

An increasing number of trait-based models has been applied to understand the impacts of climate change on ecosystem functioning and the role of functional diversity on these impacts. Nonetheless, most of the functional ecological aspects highlighted in the scientific literature remain underexplored (but see: Hofhansl et al., 2021). Few studies applying trait-based vegetation models have explored how environmental changes affect plant functional diversity *per se*, and when they do, the focus is specially on functional richness (Pappas et al., 2015; Sakschewski et al., 2016; Scheiter et al., 2013). None of them investigated how these changes affect the underlying components of functional diversity (*i.e.*, functional richness, evenness and divergence) and how these different components affect ecosystem functioning. 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 conjointly capture plant functional diversity and ecosystem functional responses to environmental changes has yet to be tested.

Building on these previous efforts, we here present a new trait-based vegetation model, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ) model. To assess the effect of including trait variability in

vegetation models, we compare two approaches of CAETÊ: a standard PFT approach that represents vegetation through three PFTs (*i.e.,* low functional diversity) and a trait-based approach (hereafter called as PLS approach) that represents a higher level of functional diversity by using 3000 combinations of trait values that seeks to express the variability of plant life strategies (PLSs) found in nature. Six traits are used to characterize the PFTs and the PLSs: C allocation and C residence time in three plant structural compartments (leaves, wood and fine roots). We compared the performance of the two modeling approaches in representing vegetation C storage and NPP for the Amazon basin region to evaluate whether plant trait diversity improves the representation of biogeochemical cycling. We also applied a scenario of reduced precipitation in the study area and by comparing model results generated from either the low-diversity (*i.e.,* PFT) *versus* the high-diversity (*i.e.,* PLS) parameterization, we assess whether the degree of plant functional diversity affects the response of ecosystem to moisture deficits using vegetation C stocks as an indicative. Additional analyses are made with PLS approach to evaluate the impacts of lower water availability on simulated functional composition and functional diversity components (richness, evenness and divergence) and its association with the impacts on C storage.

2. Material and methods

2.1. The CAETÊ model: an overview

We present an overview of the CAETÊ model and how the two used levels of diversity parametrization are defined. In this study, and for both approaches, we employed a non-transient version of the CAETÊ model, which calculates equilibrium solutions based on long-term mean monthly climate variables. The difference between the PFT and the PLS approach is only the degree of trait variability represented, the model process formulations and principles are the same for both. Each plant functional type (for PFT approach) or plant life strategy (for PLS approach) represents an average individual like in LPJ model (Sitch et al., 2003). The next section presents the procedures of model setup for this study, and the Supplementary Material SM.1 provides a more detailed description of the CAETÊ model.

For the PLS approach, the underlying premise for creating the 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 (Fig. 1; 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 representing a PLS. The values of traits that compose them are sampled from the complete range of values used as reference (see SM.1.1.1.). The volume occupied by the sampled traits can be seen as a potential functional space with tens of thousands of combinations. Like 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. On the other hand, in its PFT approach, the model's user previously defines the number of PFTs, and their traits values are based on previous vegetation models.

The physiological processes and the interaction of each PLS/PFT with the environment are determined by several functional traits, for example the maximum rate of Rubisco carboxylation (Eq. SM.16) and nitrogen to carbon ratio on plant tissues (Eq. SM.25). However, in this
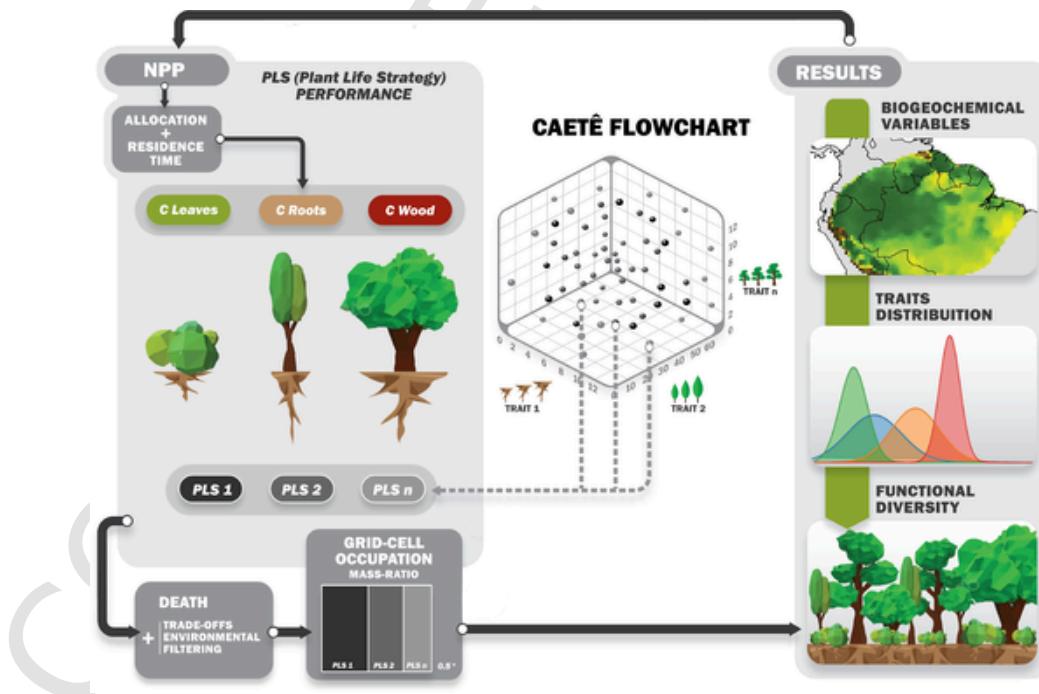

Fig. 1. Schematic diagram of the model CAETÊ in its trait-based approach. From the initial plant functional trait ranges (the axis of the hypervolume), values are uniformly sampled and combined to create hundreds of thousands of what we define as plant life strategy (PLS). The set of all created PLSs composes a hypervolume that represents the potential functional trait space in which each point inside the volume is a unique combination of functional trait values. From the potential functional trait space, 3000 PLSs are randomly sampled. Environmental filtering, the trade-offs between functional traits and the physiological processes determine the performance of a PLS (abundance), if it survives (positive carbon balance) or dies and is excluded from the grid cell. Then, the grid cell is filled as a mosaic of PLSs, in which each of them occupies an amount of space proportional to its abundance, calculated from the PLS' relative contribution to the total carbon storage in that grid cell. From the PLSs occupation, the ecophysiological variables are updated and return to the model for iteration. This modeling framework allows us to assess the model results not only regarding biogeochemical variables but also in terms of trait distribution and, therefore, the different components of functional diversity. NPP: net primary productivity; C Leaves: amount of carbon allocated to leaves; C Roots: amount of carbon allocated to fine roots; C wood: amount of carbon allocated to wood.

study six functional traits are used to distinguish each PLS or PFT. Since the analyses presented here are focused on the assessment of vegetation C storage, three traits represent the C allocation percentage of the NPP distributed to different plant tissues/compartments (leaves, fine roots and wood), and the other three traits represented C residence time in the respective plant tissues. The combination of allocation and residence time for each tissue define its C stock and, then, the total plant C stock.

The functional trait values assigned to each PLS/PFT determine its ecophysiological behavior and its responses and effects to the environment. For example, each PLS/PFT, as a distinct combination of functional traits, constitutes a differential way of storing C and capturing water and light. Thus, the functional traits of a PLS or a PFT ultimately determine its performance and survivorship. During each iteration, in a daily time step, the distinct performances of PLSs/PFTs determines the ecosystem scale processes and properties (Eq. (6)) such as GPP (growth primary productivity), evapotranspiration and C storage, which together with environmental conditions will determine the composition of PLSs and PFTs in each grid cell for the next iteration. The performance is determined as the relative abundance (Eq. (1)) of a PLS/PFT in a specific grid cell.

From now on, the symbol i refers to an average individual of a PLS or PFT, y to a grid cell and z to a plant compartment. The values for the allocation (α) and residence time (τ) traits can be found on Table SM.1 for the PLS approach and on Table SM.2 for the PFT approach. The relative abundance ($A_{r_{i,y}}$) of a PLS/PFT is the fraction of the grid cell that it occupies based on the relative contribution of this strategy to the total carbon stock in this grid cell (C_{T_y}) considering the number of living PLS/PFT (S):

$$A_{r_{i,y}} = \frac{C_{i,y}}{C_{T_y}} \tag{1}$$

$$C_{T_y} = \sum_{i=1}^{S} C_{i,y} \tag{2}$$

where $C_{i,y}$ is the carbon stock of a PLS/PFT (Eq. (3)). This procedure has support on the biomass-ratio hypothesis (Grime, 1998) which predicts that immediate effects of a species are proportional to its relative contribution to the total C storage of the community.

The $C_{i,y}$ is the sum of carbon stored ($C_{z_{i,y}}$) in each of the three plant compartments:

$$C_{i,y} = \sum_{z=1}^{3} C_{z_{i,y}} \tag{3}$$

and the $C_{z_{i,y}}$ in a certain time step t is determined by the percentage of $NPP_{i,y}$ allocated to each plant C compartment (α_{z_i}) and the carbon residence time (τ_{z_i}) in these compartments:

$$\frac{dC_{z_{i,y}}}{d_t} = \alpha_{z_i} NPP_{i,y} - \frac{C_{z_{i,y}}}{\tau_{z_i}} \tag{4}$$

$NPP_{i,y}$ is the carbon available for allocation derived from gross primary productivity ($GPP_{i,y}$; Eq. SM.3) discounting the costs of autotrophic respiration ($R_{a_{i,y}}$; Eq. SM.23):

$$NPP_{i,y} = GPP_{i,y} - R_{a_{i,y}} \tag{5}$$

From the relative abundances, it is possible to aggregate the biogeochemical variables from the PLS/PFT scale to the grid cell scale. That is, the flux or state of a variable in a grid cell is given by the sum of the values of this variable for each existing PLS/PFT (S) weighted by their relative abundance. For example, the net primary productivity in a grid cell scale (NPP_{grid_y}) is:

$$NPP_{grid_y} = \sum_{i=1}^{S} \left(NPP_{i,y} A_{r_{i,y}} \right) \tag{6}$$

Accordingly, the composition of PLSs/PFTs and their respective traits in a grid cell determine ecosystem scale processes and properties.

Each functional trait (F) is represented in a grid cell scale (F_{grid_y}) by a unique value, which is the sum of this trait value ($F_{i,y}$) calculated for each PLS/PFT alive in the grid cell, weighted by their relative abundances ($A_{r_{i,y}}$):

$$F_{grid_y} = \sum_{i=1}^{S} A_{r_{i,y}} F_{i,y} \tag{7}$$

This community weighted mean value can be understood as the dominant trait value in a community (Díaz et al., 2007).

Differential survival and performance between PLSs/PFTs are also possible because each functional trait is related to at least one trade-off (Pavlick et al., 2013; Reu et al., 2014). Trade-offs are here defined as relationships of costs and benefits that impact the ecophysiological processes of a PLS or functional type. They ultimately determine the PLS/PFT's performances and whether they will be able to deal with a specific environmental condition (Pavlick et al., 2013; Reu et al., 2011). Importantly, the trade-offs also prevent the model from enabling the survivorship of the so-called "Darwinian demons" (Law, 1979), in other words, optimal but rather unrealistic strategies that maximize all the functions that contribute to plant fitness and survival (Pavlick et al., 2013; Scheiter et al., 2013). For example, to respect mass conservation (Scheiter et al., 2013), any C investment (*i.e.*, allocation and residence time traits combination) in one tissue will always be at the expense of other: investing C in leaves can increase photosynthesis rate by increasing solar radiation absorption (Eq. SM.21 and SM.22), however, such investment is at the expense of investing in fine roots, which is responsible for water uptake, also a limiting resource for photosynthesis (Eq. SM.35). Beyond that, an intrinsic trade-off emerges from the allocation traits: per principle, their combination for all plant tissues must add up to 1 and the traits combination that do not respect this rule is excluded before model starts running (see SM.1.1.1). Carbon allocation strategies also lead to indirect competitive ability for light, what may also exclude life strategies (see SM.1.6). The ecophysiological processes linked to each functional trait, its trade-offs, and associated formulations are summarized in Table SM.3.

2.2. Simulation setup

For both CAETÊ approaches, we employed mean monthly climate variables and atmospheric CO_2 concentration 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). For the modeling experiment, the precipitation was reduced in 50% for the same 1980–2010 monthly climatology used in the control. This reduction was homogeneous: it was applied for the whole period of the study and for all the grid cells equally. We are aware that the frequency and intensity of droughts are not homogeneous over time or along environmental gradients across the basin. Furthermore, this precipitation reduction is quite severe, despite having occurred in isolated events in the past (Marengo et al., 2008) and it is also within some projections (Cox et al., 2000; 2004; Betts et al., 2004). This massive decrease in water availability is also justifiable for modeling purposes as extreme scenarios can be used to test the sensibility of ecological processes and properties simulated. Then, for this study, 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 as a mean to test our hypotheses once the effects of extreme drought events to ecosystem processes and biodiversity it is still not entirely clear (Allen et al., 2010).

For the PFT approach we defined 3 tropical PFTs, and their traits values were chosen based on those used by other vegetation models (Table SM.2). For the PLS approach we used 3000 PLSs, and this number was defined based on a sensitivity test (see Supplementary Material SM.2). The ranges of values of each functional trait considered in this approach were based on empirical/experimental literature and are presented in Table SM.1

In both approaches, all grid cells are initialized with the same set of PLSs or PFTs, under conditions that are analogous to bare soil. However, in each grid cell the PLSs/PFTs will perform differently such that some strategies will survive, each of them occupying a different portion of the cell, while others will be excluded from the spatial grain in the simulation and cannot be reestablished. Importantly, for this study, there is no repopulation of the PFTs or PLSs excluded. Rather, the model is run until equilibrium with 3000 PLSs/3 PFTs and regular climate condition and, after, it is run again with the same 3000 PLSs/3 PFTs but with reduced precipitation. That is why it is possible that PLSs/PFTs can be excluded with regular climatic conditions but increase/decrease their abundance with reduced precipitation.

Before the model execution a model initialization phase is performed: (i) to determine the initial C content in plant compartments and it is run until the attaining the stability attained for the total C stock (*i.e.,* the sum of C in all plant compartments) in all the grid cells (see details in SM.1.1.2); and (ii) to check the viability of each newly created PLS (see SM.1.1.1). After the initialization phase, the model runs by continuously repeating the input data series (under regular climate or under reduced precipitation) until the stability of simulated results was attained.

2.3. CAETÊ performance evaluation

The performance of the two modeling approaches in representing the spatial distribution of vegetation C storage and NPP in the Amazon region was compared with reference data. For C storage we used data from Baccini et al. (2012) and Saatchi et al. (2011); and for NPP the data came from MODIS NPP Project (MOD17A3; Running and Zhao, 2021). These comparisons were made under current climatic conditions (1980 – 2010). We considered that 47.5% of living dry biomass from reference data is comprised of C (Thomas and Martin, 2012). Following the reference data, only the aboveground component was considered. For the model performance evaluation, we estimated the absolute difference between maps from CAETÊ simulations and maps from reference data and a scatterplot analysis was performed to identify the trends in the model approaches simulations.

2.4. Assessing functional diversity and composition

In this study we focused on large-scale analyses of functional diversity and its components across the Amazon basin. It means that trait distributions used to evaluate functional diversity corresponds to the distribution of the set of dominant trait values obtained for each grid cell, as explained in Section 2.1 (Eq. (4)). As mentioned in the introduction, using only a small number of PFTs to represent variability precludes access to functional diversity analyses. Hence, functional diversity analyses are here limited only to the PLS approach.

Functional diversity and functional composition of communities were analyzed both considering each functional trait independently (single-trait analyses) and the combinations of traits (multi-trait analyses). The single-trait and multi-trait analyses allow a broader 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.

In the single-trait analyses, distribution curves were generated by using the functional traits' occurrence following the study by 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 calculated through probability density distributions, *i.e.,* the trait probability density distributions. From these distributions, we assessed the three functional diversity components as defined by Carmona et al. (2016): (i) functional richness: the amount of functional space occupied by the community, *i.e.* the total range of trait values for a specific functional trait considering all organisms (PLSs in our case); (ii) functional evenness: the regularity of the density distribution of the PLSs' trait values in the functional trait space; and (iii) functional divergence: the degree to which the abundance of trait values of PLSs are distributed toward the extremes of their functional trait space.

For the multi-trait analyses, 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, the 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 evaluate 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, we were able to fulfill the statistical assumptions for constructing the hypervolumes.

Despite the focus of our analyses being on the basin scale, we made some additional functional diversity analyses on a finer scale using three spatial windows of 10×10 grid cells each along a northwest to southeast axis (Fig. SM.2). Looking into finer scales enables the evaluation whether the results obtained from the whole amazon basin scale analyses are not only a product of the natural environmental heterogeneity, once the basin is well known to present a large-scale variation in climatic and edaphic properties (Ter Steege et al., 2006; Quesada et al., 2012; Sombroek, 2000).

2.5. Assessing effects of decreased precipitation

In the experiment of 50% reduction in precipitation, we compared the degree of change in C stock between the two modeling approaches used in this study to evaluate if trait variability influences C storage under environmental change.

Further, from the results simulated by the PLS approach we also evaluated the role of the different components of functional diversity in this change. For this, we assessed whether the plant communities were functionally reorganized in the scenario of reduced precipitation by computing the dissimilarity index (degree of overlap) between the trait probability density distributions from the regular climate scenario and those from the reduced precipitation scenario (Carmona et al., 2016). This index varies from 0 (completely functionally similar; overlapping density curves) to 1 (completely functionally different; no overlap). To estimate the changes in hypervolumes due to precipitation reduction we computed their overlap degree through the Jaccard similarity index, which ranges from 0 (completely different; no overlap) to 1 (completely similar, overlapping hypervolumes). In addition, we assessed whether a centroid displacement occurred with the applied precipitation reduction. The displacement indicates how much the mean values of the communities were dislocated from their previous location within the hypervolume. To test the degree of communities' functional reorganization we analyzed the changes in trait abundance throughout the functional space generated by the trait probability density distributions. From this analysis we were able to observe, for example, the exclusion

of trait values and/or the increase in the occurrence of trait values that were rare under regular climatic conditions. To understand the impacts of precipitation reduction on functional diversity facets (richness, evenness, and divergence) for the single-trait analysis, we computed the percentage change in their values between regular and reduced precipitation climatic conditions. For the multi-trait analysis, we compared the hypervolume sizes before and after the reduced precipitation application once change in volume sizes represents a shift in the community functional richness. We also performed these analyses for the finer scale: we estimated the change in trait distributions with reduced precipitation using the same method described before (for single and multi-traits), but, in this scale, with focus on the functional reorganization of the community and on functional richness.

3. Results

3.1. CAETÊ model performance evaluation

Within the studied region, the PFT approach simulates 127.9 Pg C stored in aboveground C and the PLS approach simulates 86.0 Pg C, while Baccini et al. (2012) estimates 80.2 Pg C of total aboveground C stock and Saatchi et al. (2011) estimates 71.7 Pg C. In terms of spatial patterns in vegetation C storage, both modeling approaches show over- or underestimation in the values simulated. The overestimation is especially concentrated in naturally drier areas, for example in North-Western Amazonia. We also observed an overestimation along the basin edges, which are known as regions of transition to drier areas, fire-prone vegetations and subject to the intensive land use (Haghtalab et al., 2020; Morton et al., 2013; Nobre et al., 2016). However, the CAETÊ

in its PFT approach tends to show the overestimation in a much higher degree and in more locations throughout the basin, with emphasis on the central region and basin edges when compared to the PLS (Fig. 2). On the other hand, the PLS approach tends to underestimate mean C values in some regions, for example, in the east and southwest parts of the basin. The PLS approach presented more areas with no differences between simulated and reference values, (white cells in Figs. 2b and e) and a higher number of points closer to the 1:1 line in the scatter plot (Fig. 2c and f) thereby matching the values used as reference reasonably well.

The CAETÊ model simulated a total annual NPP of 122.3 Pg C yr^{-1} (PFT approach) and 76.0 Pg C yr^{-1} (PLS approach) for the Amazon basin. MODIS-based estimation is 74.6 Pg C yr^{-1} (Running and Zhao, 2021). By comparing the NPP simulated by CAETÊ with remote sensing NPP estimations (MODIS; Running and Zhao, 2021), the PLS approach revealed a reasonably good ability to capture broad spatial patterns of remotely sensed NPP estimations (MODIS; Running and Zhao, 2021; Fig. SM.3b and SM.3c), despite an underestimation in the Andean region and a small overestimation in the northwest/central basin region. In contrast, using a small number of PFTs resulted in a widespread and prominent overestimation for this variable (Fig. SM.3b and SM3c), except for the underestimation in the Andean region.

3.2. Carbon stocks under reduced precipitation

The 50% reduction in precipitation caused a widespread decrease in C stocks throughout the basin in both model approaches (Fig. 3a and b). When considering the whole basin, total C loss was equal to 73.48 Pg C and 49.43 Pg C for the PFT and PLS approach respectively, representing
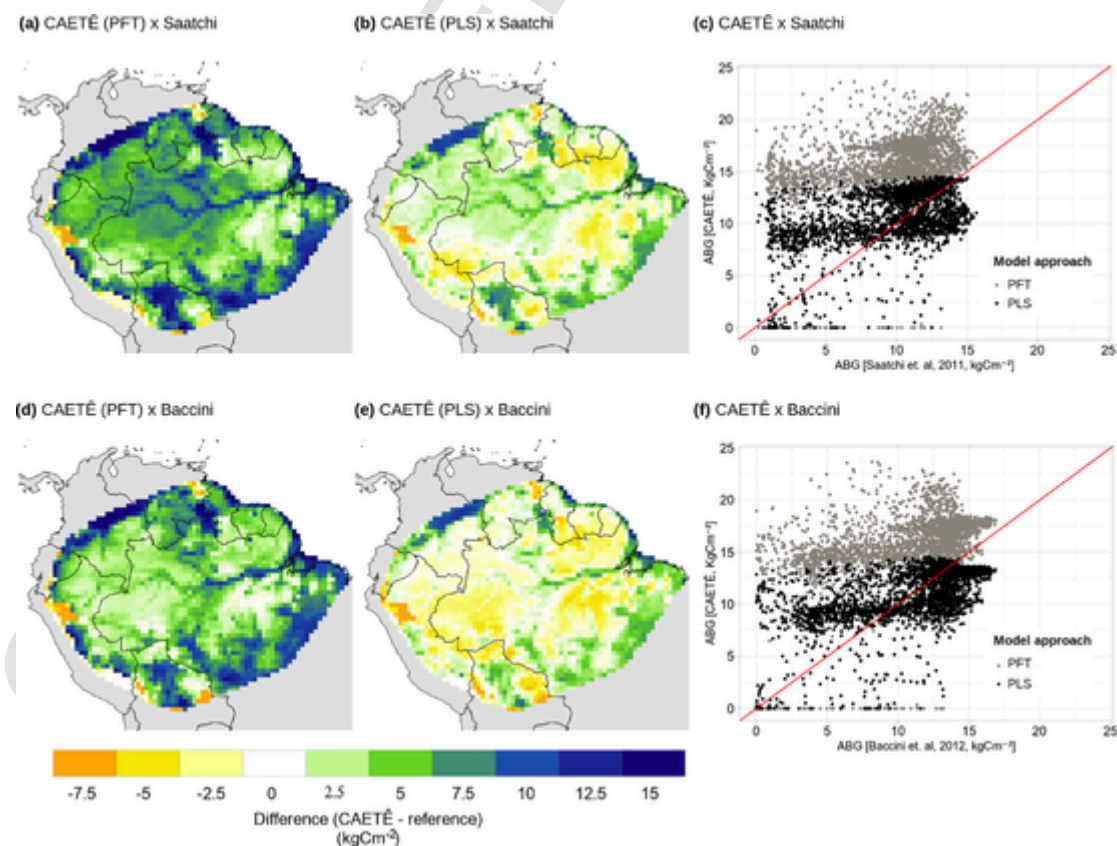

Fig. 2. Evaluation of CAETÊ performance in representing aboveground carbon storage for both modeling approaches, PFT and trait-based approach, when compared to two reference maps: Baccini et al. (2012) and Saatchi et al. (2011). The plots (a), (b), (d) and (e) show the spatial absolute difference between values simulated by CAETÊ and those simulated by references. The plots (c) and (f) show the linear regression between CAETÊ and reference maps for all the simulated grid cells. The 1:1 line is represented in red. AGB: aboveground carbon storage. The carbon projected by CAETÊ can be found in the Supplementary Material (Fig. SM.8). PFT: PFT approach. PLS: trait-based approach.

Total carbon

(a) CAETÊ (PFT)   **(b)** CAETÊ (PLS)

Fine roots carbon

(c) CAETÊ (PFT)   **(d)** CAETÊ (PLS)

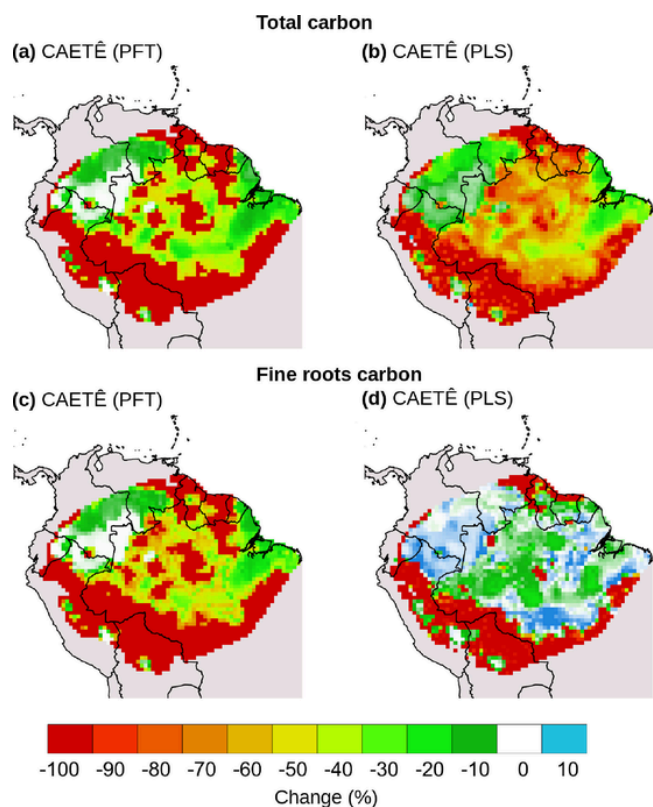-100 -90 -80 -70 -60 -50 -40 -30 -20 -10 0 10
Change (%)

Fig. 3. Percentage change in total carbon stock (a and b) and in fine roots carbon stock (c and d) after reduced precipitation application (−50%) for the two employed modeling approaches: PFT and trait-based approach. The change of carbon storage in the compartment of leaves and wood can be found in the Supplementary Material (Fig. SM.4). PFT: PFT approach. PLS: trait-based approach.

a similar percentage decrease compared to regular climatic conditions: −57.75% for PFT and −57.48% for PLS approach. However, the spatial pattern of change was significantly distinct. The PLS approach was able to maintain C stocks in several grid cells where none of the PFTs survived in the PFT approach. This difference is more evident in central Amazon and naturally drier areas, such as in the transition between the Amazon forest and the Cerrado savannah in the southeast. Furthermore, the C losses simulated by the PLS approach presents a smoother gradient between a grid cell value and its neighboring cells and across different basin regions, unlike in the PFT approach, which shows more abrupt differences between grid cells. Surprisingly, in grid cells where both modeling approaches maintained at least a minimum C stock, the PFT approach presented higher values when compared to those from the PLS one (Fig. 3a and b).

Specific plant compartments also showed distinct patterns of changes when comparing the employed modeling approaches (Fig. 3c and d for fine roots, Fig. SM.4 for leaves and wood). None of the compartments showed an increase in C stock with precipitation reduction, except for the fine roots compartment in the simulation with the PLS approach (blue areas in Fig. 3d), such an increase is more apparent in the transition between the Amazon and Cerrado and in the northeast part of the basin. The increased investment in fine roots resulted in a rise in the root:shoot ratio for the PLS approach, with an average increase of 74.7%, in contrast to an average decrease of 7.7% for the PFT approach.

3.3. Effects of reduced precipitation on functional composition

After applying the precipitation reduction, we found high dissimilarity index values (close to 1; Table 1) owing to changes in the trait probability density distributions for the six plant functional traits (Fig. 4). These dissimilarities degrees indicate that the communities significantly changed in terms of their structure and composition under moisture stress. For example, trait composition shifted away from hyperdominance (decrease in the peaks of the curves) of a previously restricted range of values toward a density increase in other trait values that were previously rare (very low density) or absent (Fig. 4). Additionally, the traits in the hypervolumes presented a pronounced modification in the way they occupy the functional space (Fig. 5): the overlap degree between the hypervolumes of the two climatic scenarios yielded a value of 0.038 when considering the whole Amazon. Finally, the centroid showed a displacement after imposing the climatic alteration, indicating a change in the communities' mean values and compositions (Fig. 5).

Beyond that, with lower water availability, the distribution of the single-traits along the functional space showed a higher diversity of values that presented an increase in density, that is, a higher probability of occurrence, which resulted in a much more diffuse distribution within the functional space (Fig. 4). The same pattern of distribution along functional space observed for single traits arose when considering all traits combined through the hypervolumes: an increase in the functional space occupation by the traits (Fig. 5). The increase in density was observed in traits with higher carbon allocation values to fine roots, lower carbon allocation to leaves and to wood (Fig. 4a, b and c). Also, higher values for carbon residence time in leaves and fine roots but a decrease in wood (Fig. 4d, e and f).

Regarding the analyses in the finer scale, our results show the same pattern that was found when considering the large scale (the whole Amazon basin): an increase in the occupation of the functional space for all the six functional traits in their probability distributions (Fig. SM.5 and SM.6) and an increase in the volume occupied when considering the six traits together (Fig. SM.7). The high dissimilarity indices between trait probability density distributions with regular climate and decreased precipitation (Table SM.4), together with the small overlap between hypervolume, indicate that as well as found in the Amazon basin scale, the communities in the three 10×10 grid region underwent a functional restructuration.

3.4. 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 (Fig. 6). Functional richness and functional evenness increased in a level higher than 100% for all the six considered traits. Divergence had an increase of more than 200% for the leaf allocation trait, while the other traits displayed a reduction in this facet (Fig. 6c). From a multi-trait perspective, there was an increase in richness due to the enlargement in the volume occupied by the communities within the functional space (Fig. 5): under current climatic conditions, the size of the volume that the data occupied

Table 1

Dissimilarities of trait probability density distributions (Fig. 4) with the applied reduction in precipitation (−50%) for the PLS approach. The closer the value is to 1, the more dissimilar the curves are to each other.

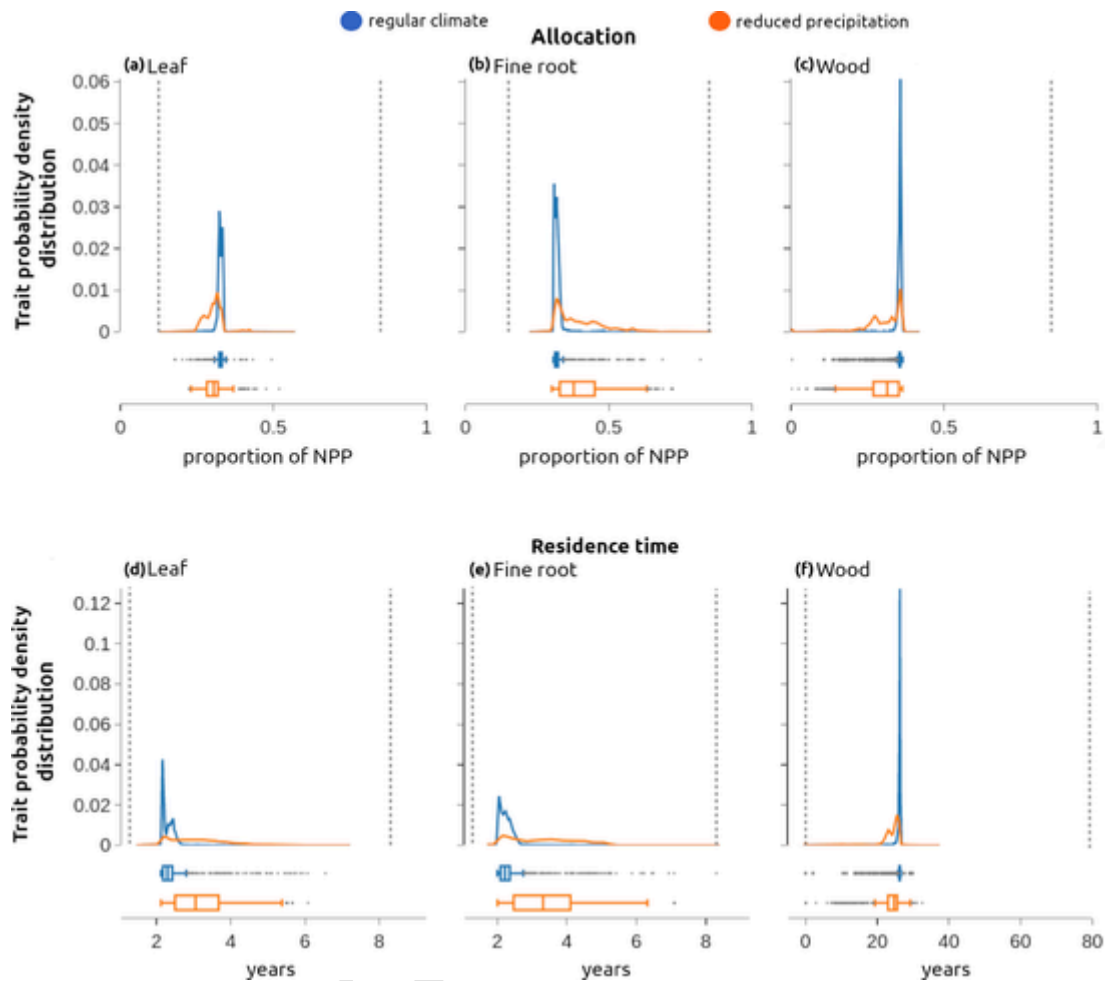| Functional trait	Distribution dissimilarity
leaf allocation	0.680
root allocation	0.656
wood allocation	0.638
leaf residence time	0.678
root residence time	0.664
wood residence time	0.755

Fig. 4. Density distributions of functional traits using the trait probability density method (Carmona et al., 2016) for the trait-based approach. The curves correspond to the probability density distribution of trait values across the Amazon basin. Each boxplot represents the median value and variance for each trait in each climatic condition. The boxes extend from the first to the third quartiles, and the whiskers extend from the minimum and maximum data. The outliers are shown in gray dots. The orange curves/boxplots represent the results with the applied low precipitation scenario, and the blue curves/boxplots represent the results concerning the regular climate conditions. The plots from (a) to (c) show the results concerning the allocation traits, and the plots from (d) to (f) display the results for the residence time traits. NPP: net primary productivity. The dissimilarities between the distributions before and after the reduced precipitation are presented in Table 1. Note that the scales of the y and x axes are different for allocation and residence time traits. The graphs are presented in this way to improve readability. The gray dotted lines represent the initial possible range of values for each trait (showed in Table SM.1). The plot (c) only shows one dotted line since the grass strategies present no allocation to wood tissues, hence the line in the point 0 overlap the y axes.

was equal to 1.71 while under reduced precipitation we found a volume size of 47.84.

On the finer scales, like in the whole basin, an increase in the range of trait values (Table SM.4) and in the volume occupied when considering the six traits together (Fig. SM.7) indicate a rise in functional richness. Beyond that, the curves from the trait probability density distributions (Fig. SM.5 and SM.6 and Table SM.4) showed a high distribution dissimilarity (~1) and the hypervolumes (regular climate and reduced precipitation) presented a small overlap for the three analyzed regions: 0.006, 0.001 and 0.007 for the northwest, the center and the southeast respectively.

4. Discussion

4.1. Model performance

Our results indicate that the inclusion of trait variability in vegetation models may lead to considerable improvement when simulating the vegetation C cycle with current climatic conditions. Compared to reference data (Fig. 2 and SM.3), our simulations with the PLS approach

were able to represent NPP and vegetation C storage reasonably well and showed better agreement (spatial distribution and total values) than the PFT approach). Improved accuracy in biogeochemical variables has already been observed in other PFT-based models when trait variability was added (Fyllas et al., 2014; Sakschewski et al., 2015; Verheijen et al., 2013). Trait variability confers a higher diversity of community responses to environmental filtering through climatic heterogeneity, thereby allowing a more realistic simulation of plant community assembly (Keddy, 1992) avoiding a complete switch in vegetation state, such as a catastrophic Amazon dieback (Lapola et al., 2018), due to abrupt changes in plant performance and establishment success (Fyllas et al., 2014; Sakschewski et al., 2015; Scheiter et al., 2013).

Both modeling approaches show some mismatch with regard to the reference maps, such that there appears to be an overestimation of aboveground vegetation C storage and NPP, and especially so for the PFT approach (Fig. 2 and SM.3). This is because 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
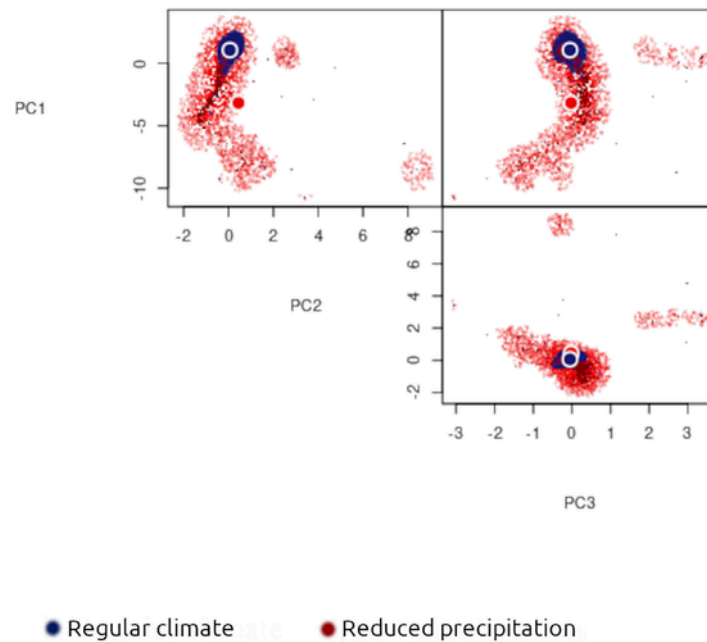
Fig. 5. Hypervolumes created with the six functional traits together through the method of Blonder et al. (2018). The volumes here represented refer to the trait-based modeling approach simulations. The hypervolumes were created after the data were submitted to a PCA (see Fig. SM.10). The blue points indicate the data in a regular climate scenario, and the red points indicate the scenario of −50% of precipitation in the study area. The darker the color of the point, the higher the density of the value within the functional space. The bigger circles represent the centroid (*i.e.*, the mean values) of data distribution.

vegetation C storage (Scheiter et al., 2013; Verheijen et al., 2013). Furthermore, both approaches show a tendency to overestimate vegetation C storage and NPP at the edges and in the central/northwestern Amazon basin (Fig. 2 and SM.3). These inconsistencies could be attenuated through the improvement of some caveats of the CAETÊ model. First, such an overestimation can be linked to the lack of representation of human land use and fire for determining vegetation distribution in the model (Houghton et al., 2001; Saatchi et al., 2007). Another important caveat is that the model does not yet represent impacts on vulnerability to cavitation and embolism (Anderegg et al., 2016; Oliveira et al., 2021). The lack of representation of human land use, fire and plant hydraulics may be particularly important to achieve a more realistic representation of C storage in the edges of the basin (Eller et al., 2018; Joshi et al., 2020; Papastefanou et al., 2020; Rowland et al., 2015). Furthermore, nutrient cycling (nitrogen and phosphorus) is not represented in our model and low soil nutrient availability in the Amazon may limit vegetation C storage across the Amazon basin (Fleischer et al., 2019; Yang et al., 2019).

It is important to highlight that despite using the maps produced by Saatchi et al. (2011) and Baccini et al. (2012) as reference, these maps include other sources of uncertainties (Mitchard et al., 2013) and therefore present different estimates of aboveground biomass across the Amazon basin.

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

We found that, in accordance with previous literature (Enquist and Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019), the inclusion of trait variability in vegetation models in fact matters for projecting the impacts of environmental change in ecosystems. Although the two approaches applied in this study (*i.e.,* PFT *vs.* PLS) show similar changes with regard to total basin vegetation C budget, spatial patterns showed that only considering this biogeochemical variable can hide important details about the mechanism in which trait diversity determines ecosystem functioning. For example, the inclusion of trait variability in the model avoided sharp boundaries (especially in naturally) in drier

regions, showing a more subtle, less sensitive, and probably more realistic change in C stock across the basin (Fig. 3) when compared to models PFT based that commonly simulate the Amazon dieback (Cox et al., 2000, 2004; Lapola et al., 2009; Oyama and Nobre, 2003).

Disturbances are expected to trigger 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 for the PLS approach: 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 were significantly modified by the climatic forcing scenario. This ability to functionally reorganize and cope with new climatic conditions in the PLS approach (allowed by trait variability) was decisive to the effects of reduced precipitation on both the total and the spatial distribution of C vegetation storage. Trait variability allows for functional density compensation process that counterbalances losses or decreases in the dominance of plant life strategies, thus decreasing the impact of perturbation on ecosystem functioning (Gonzalez and Loreau, 2009; Mori et al., 2013; Sakschewski et al., 2016). On the other hand, in the PFT approach, alternative PFTs are too few to compensate for losses in establishments, hence, this model approach prevents better suited trait combinations to establish, leading to higher occurrence of grid cells in which none of the PFT's survived (Fig. 3). This severe effect of environmental change using a PFT approach corroborates other modeling studies (Huntingford et al., 2013; Sakschewski et al., 2016). Our results reinforce the importance of functional diversity for maintaining ecosystem functioning and give support for the "insurance hypothesis" (Mori et al., 2013; Yachi and Loreau, 1999), thus strengthening the assumption that diversity can promote ecosystem stability (Tilman et al., 2006).

4.3. Functional composition and the selection of plant life strategies

The changes in functional composition and structure due to reduced precipitation in the PLS simulation is supported by the dissimilarity/similarity indices found between the trait probability density distribu-
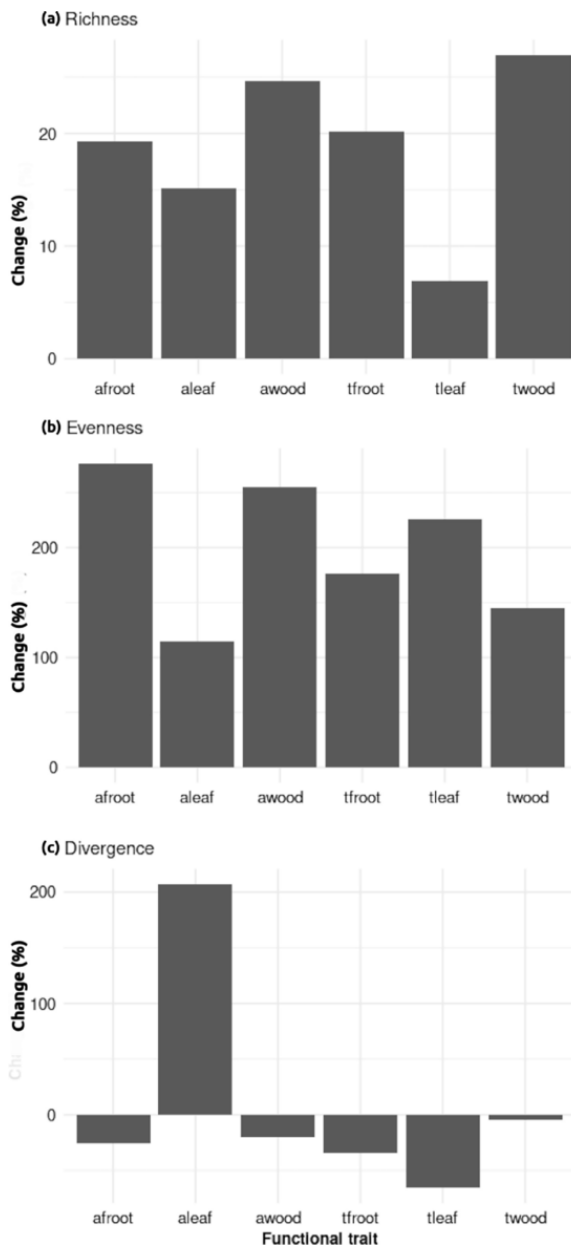
Fig. 6. Percentage change in the functional diversity components (divergence, evenness and richness) with the applied precipitation reduction scenario (−50%) for the trait-based modeling approach. This results concern to the Amazon basin spatial scale. Allocation to fine roots (afroot), leaves (aleaf) and wood (awood). Carbon residence time for fine roots (tfroot), leaves (tleaf) and wood (twood).

tions and the hypervolumes, respectively. The centroids' displacements also showed that the dominant values (composition) were modified with the new climatic condition. This high capacity of communities in the PLS approach simulations to functionally reorganize enabled shifts in functional community composition, thus corroborating with the hypothesis of a selection toward plant strategies with higher investment in roots in drier climate conditions (Fig. 4b and e). The higher investment in roots simulated by the PLS approach was to the detriment of investment in leaves (Fig. 4a and d) and woody tissue (Fig. 4c and f), thus leading to higher root:shoot ratios. Higher root biomass enabled water uptake and allowed the community of the PLS simulation to better deal with the imposed moisture stress and maintain C stocks or reduce the degree of biomass loss when compared to the simulation using PFTs. The prioritization of root investment at the expense of other tissues in

response to drought has been observed in manipulative ecosystem experiments and from monitoring forest inventory plots (Doughty et al., 2014; Kannenberg et al., 2019; Rowland et al., 2014). Given the limited trait variability, the PFT approach did not show these changes in C investment, increasing mortality rates and preventing the PFTs from establishing in some grid cells, thereby rendering the ecosystem more vulnerable in general (Fig. 3a), as predicted.

Notwithstanding, an unexpected result was that in some grid cells the amount of C stock in the PFT was higher than that in the PLS approach with the applied reduced precipitation (Fig. 3a and b). This occurred due to an increase in the root:shoot ratio in the simulations with high trait variability, that is, C was allocated toward pools with shorter turnover times (fine roots), which result in less total vegetation C storage (Chave et al., 2009; De Kauwe et al., 2014). Although the increase in fine roots in the PLS approach provides resistance to moisture stress, thereby preventing the total loss of carbon in several grid cells, it also led to lower vegetation C storage (in some locations) compared to the PFT approach. This result is contrary to the widely accepted paradigm that higher functional diversity maximizes ecosystem function (Cadotte, 2017; Tilman et al., 1997; Tilman et al., 2014). Our findings of the community-wide reorganization and associated increase in trait variability in response to novel climatic conditions indicate that functional diversity *per se* does not necessarily maximize ecosystem functions and properties such as C storage (Chiang et al., 2016; Holzwarth et al., 2015) but that functional diversity can influence ecosystem functions in more than one direction (Hooper et al., 2005; Shen et al., 2016). In our study, the functional composition, and especially the dominant plant functional trait, was more critical in determining the C stock than functional richness, with other studies finding similar results (Chiang et al., 2016; Finegan et al., 2015; Ruiz-Jaen and Potvin, 2011; Roscher et al., 2012). Overall, this suggests that trait-based modeling approaches can improve our mechanistic understanding of the linkage between functional diversity and ecosystem functioning.

4.4. Environmental changes modify functional diversity components

Our results from analyses of the PLS approach showed that a reduction of precipitation modified the way that traits occupy the functional space (Fig. 4 and 5) and, as consequence, the functional diversity facets (Fig. 6). For example, reduced precipitation led to a wider range of expressed trait values in functional space (Fig. 4 and 5) and thus increased the community's richness (Fig. 6a). This increase in functional richness contradicts the expected outcomes from the environmental filtering hypothesis (Keddy 1992; Grime 1998; Boersma et al., 2016; Funk et al., 2017; Perronne and Gaba, 2017). Our findings may be explained by a decrease in hyperdominance in response to simulated climate change, which allowed a higher range of ecological strategies to become viable, in accordance with the compensatory dynamics theory (Gonzales and Loreau, 2009; Walker et al., 1999). Importantly, these results provide further evidence that environmental filtering not always reduce trait diversity (Le Bagousse-Pinget et al. 2017; Laughlin and Laughlin 2013) and that functional richness can increase after disturbance, especially so if environmental change mainly affects the dominant plant functional strategies (Boersma et al., 2016; Funk et al., 2017; Mouillot et al., 2013a). Beyond that, it is necessary to consider that the role of the environmental filtering as a driver of functional structure will strongly depend on the traits being considered (de La Riva et al., 2017).

The observed increase in functional richness is also certainly linked to the CAETÊ functioning mechanism. Model experiment of reduced precipitation resulted in higher functional richness mainly to the increase in the range of traits values of traits related to roots C allocation and residence time, which in turn, thanks to the considered trade-offs, was metabolically balanced by increases in functional richness related to other traits. In addition, one could hypothesize that the overestimation of C storage in drier regions at the edges of the Amazon basin

would be the cause of higher simulated functional richness under reduced precipitation. However, it is more reasonable to first consider that, at the community scale, higher C stock may not be directly linked to functional richness. For instance, we found that despite the model simulates higher value for total C in the northwest of the Amazon basin, this region also showed lower functional richness than the southeast for all the functional traits, beyond a smaller increase of functional richness with reduced precipitation (Table SM.4 and Fig. SM.5 and SM.6), and the concentration of trait values in certain restricted areas of the functional space/volume could be one of the causes of such pattern.

There was an increase in evenness in all traits considered in the PLS approach (Fig. 6b). The evenness increase is tightly related to the observed decrease in dominance and increase in the abundance of trait values that were very rare in regular climate condition. Evenness can also be interpreted as evidence of the effectiveness of using the functional niche space; the higher the evenness is, the higher the utilization of the total functional space is (De La Riva et al., 2017; Hillebrand et al., 2008; Mouillot et al., 2011). Therefore, our results indicate that a change in the environment can force the community to better occupy the functional niche space, thus providing a lower sensitivity to the applied reduced precipitation, if the community presents sufficient variability in its trait values.

We observed a general decrease in divergence (Fig. 6c), which was caused by the strong decrease in abundance of previous dominant trait values which tended to concentrate at the extremes of functional spaces with the regular climate condition. Consequently, other trait values, concentrated along the functional axis, that were not as abundant became significant for the community after the reduction in precipitation. 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 a declining in the abundance of specialist species that were the most impacted by the disturbance. In addition, this decrease in divergence can be additional 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).

It could be argued that the observed changes in functional diversity, especially the increase in functional richness, can be attributed to the fact that we considered the whole Amazon basin as a single ecological unit while it is known that a high environmental heterogeneity exists throughout the basin. However, a similar pattern was found across a gradient of precipitation sampled from the northwest, center and southeast of the Amazon basin (Fig. SM.5, SM.6 and SM.7). This finding highlight that our results are not dependent on the spatial scale of analysis or the degree of environmental heterogeneity. Nevertheless, to avoid a simplification of diversity when considering large spatial scales, we recommend that future studies should try to integrate functional diversity across spatial scales, in this case from grid cells to the whole Amazon basin, as described in Carmona et al. (2016).

5. Concluding remarks

In this study, we show that incorporating trait variability in a vegetation model improves accuracy in representing ecosystem functioning and also plays an import role on ecosystem response to climate change. The trait-based modeling approach allows for a more in depth analysis on the mechanisms that connect ecosystem functioning and the different components of functional diversity. With the PLS approach, we show that the traits diversity allows the community to functionally reorganize under environmental changes, occupying a greater amount of functional space and increasing the occurrence of strategies that deal better with the applied lower water availability (higher investment in fine roots). Investment in roots at the expense of investment in leaves and wood led to a relatively lower total carbon storage. Functional reorganization also triggered changes in the primary components of func-

tional diversity: increase in richness and evenness, and decrease in divergence. On the other hand, the use of a small number of PFTs restrict changes in the functional structure of the community, leading to a more expressive impact of environmental change on ecosystem functioning. In addition, PFT approach hinders the assess to functional diversity analyses.

This study brings further evidence that the inclusion of trait variability may have implications for modeling the so-called Amazon tipping point (Lovejoy and Nobre, 2018) since a trait-based-like approach would potentially yield more subtle, but not necessarily less relevant, responses of the forest vegetation to extreme climate change (Sakschewski et al., 2015).

Data availability statement

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

Uncited references

CRediT authorship contribution statement

Bianca Fazio Rius : Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **João Paulo Darela Filho :** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – review & editing. **Katrin Fleischer :** Conceptualization, Writing – review & editing. **Florian Hofhansl :** Conceptualization, Writing – review & editing. **Carolina Casagrande Blanco :** Conceptualization, Validation, Writing – review & editing. **Anja Rammig :** Writing – review & editing. **Tomas Domingues :** Writing – review & editing. **David Montenegro Lapola :** Conceptualization, Methodology, Validation, Resources, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2023.110323.

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