Katrin's suggestions:

-improve readability, shorten the text, avoid redundant information

- also some paragraphs can be completely taken out or some info merged with others

- the discussion seems very long in comparison to the other sections

-I found that you focus on Carbon storage in your model result but do not exploit more

analysis on that - like you could give actual numbers of biomass compartment changes,

also per region, until now you mostly describe that qualitatively

- on the carbon storage changes, I suggest that you talk a lot more and lot earlier about

the underlying processes. You have 6 variable traits, so they cover a certain functionality

which makes some strategy be more or less successful, leading to more or less carbon

storage, only sticking to discussing C storage change without consistently linking the

processes involved is not very meaningful - you have a trait-based approach so talk

about the associated trait-function relationships.

-the models reach the same C storage change after drought : if you give more

quantitative detail on the individual compartment/regional changes and the underlying

processes would give a lot more context on this result

-And as Anja noted, be careful with "drier climate" - climate change will change temperature,
VPD, radiation, and precip. you are looking at one aspect, a discussion thereof could also be
useful - perhaps when saying that future model development will consider leaf-level
responses to atmospheric conditions / hydraulic failure - then these aspects of CC will be
important to assess.

you can benefit now from streamlining your manuscript: i.e. focus on what is really the
outcome of your study and the underlying processes. You have a limited number of traits that
vary, that is okay, but then make sure you rightfully exploit and analyze the aspects of change
that your model can capture. And then discuss what will need to come next to consider the
most important traits we need to model functional changes in response to CC.

-REMEMBER TO INTEGRATE YOUR CONTRIBUTIONS IN A BROADER CONTEXT

Maybe create some maps of traits distribution?

Bianca Rius
03/29/2021 12:06

For example:
-this type of model helps to look into functional diversity effects, responses that can really help to seek still open ecology issues (eg., biodiversity-ecosystem relationship)
-you can indicate which type of processes/traits are missing in your study
-look BEYOND biogeochemical properties

Bianca Rius
03/29/2021 12:15

30 **- FOCUS YOUR PAPER ON ONE CENTRAL CONTRIBUTION: your struggle to find**

31 **this balance may appropriately result in"one contribution" that is multifaceted. For**

32 **example, a technology paper may describe both its new technology and a**

33 **biological result using it; the bridge that unifies these two facets is a clear**

34 **description of how the new technology can be used to do new biology.**

35

36 **Modeled changes in Amazon forest plant functional diversity and vegetation carbon**

37 **storage in response to** reduced precipitation~~drought~~**: a trait-based vs. a plant functional**

38 **type approach**

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56

57 **Abstract**

58 The impact of projected climate change and increasing frequency of drought periods on plant

59 functional diversity and the associated Amazon forest carbon sink remain poorly understood.

60 Foregoing studies suggest that while changes in functional richness, divergence and evenness

61 might affect ecosystem carbon stocks other ecosystem properties like vegetation structure

Visto o comentário da Anja sobre seca
Bianca Rius
03/26/2021 11:49

Put the other authors
Bianca Rius
03/19/2021 14:22

62 remain unchanged. Here we investigate how a 50% reduction in rainfall affects plant

63 functional diversity and associated vegetation carbon stocks across the Amazon basin. We

64 applied a modeling approach where functional diversity may or may not be predefined: (i) a

65 plant functional type approach (PFTA; fixed trait values in 3 tropical PFTs) and, (ii) a varying

66 trait-based approach (TBA; semi-random combination of trait values creating 3000 plant life

67 strategies). Six functional traits were considered as fixed/variant: carbon allocation and

68 residence time of leaves, aboveground woody tissues and fine roots. The imposed <mark>drought</mark>

69 caused a widespread loss of carbon storage in both approaches (with a similar magnitude of

70 reduction of around 60%). However, the spatial pattern differed, with TBA showing more

71 subtle changes along the basin, mainly on its southern limits. Also, the TBA presented an

72 increase in fine roots investment (~10%), whereas the PFTA reduced carbon in all plant

73 compartments. Changes in functional diversity were different in magnitude and direction

74 between respective approaches: TBA(PFTA) showed changes, for fine roots allocation, of

75 +19.33%(+4.94%) in richness; +276.54%(-74.71%) in evenness and -26.01%(+0.15%) in

76 divergence, resulting in a functional reorganization of the plant community allowing

77 previously rare trait values to increase its density and a change in functional composition. Our

78 results demonstrate that the inclusion of higher functional diversity did not show a significant

79 difference in total carbon loss, mainly because the carbon assimilation processes

80 (photosynthesis and respiration) did not differ between the different modeling approaches.

81 However, the opposing results regarding carbon allocation and residence time suggest that

82 varying-trait vegetation modeling offers a promising, though still underexplored, method to

83 represent and better understand changing functional diversity and plant-trait distribution in

84 light of biogeochemical processes that currently applied DGVMs do not cover.

85 **Keywords:** trait-based modeling, climate change, carbon allocation, functional composition,

86 functional richness, functional evenness, tropical forest

Introduction

88 The projected decrease in the Amazon forest's ability to absorb and store carbon due to

89 climate change is permeated with uncertainties (Finegan et al., 2015), and the role of

90 functional diversity (the values, ranges of values and relative abundance of functional traits in

91 a given community or ecological unit; Díaz et al, 2007) on this ecosystem process is poorly

92 explored (Esquivel-Muelbert et al., 2017; 2018; Poorter et al., 2015; Sakschewski et al., 2016;

93 Sitch et al., 2008). Dynamic Global Vegetation models (DGVMs) have been widely used to

94 explore the impacts of climate change in Amazon forest from a biogeochemical perspective

95 (Cramer et al., 2001; Scheiter, Langan, & Higgins, 2013) providing substantial contribution to

96 our current knowledge of the Amazon forest ecology and resilience (Díaz & Cabido, 1997;

97 Prentice et al., 2007; Scheiter, Langan, & Higgins, 2013). For instance, the projected

98 possibility of a large-scale degradation of the Amazon forest driven by severe climatic

99 changes (Cox, Betts, Jones, Spall, & Totterdell, 2000) and the role of soil phosphorus as a

100 limiting factor to CO_2 fertilization in the region (Fleischer et al., 2019), are typical results

101 derived from studies using DGVMs.

102 Nonetheless, model projections regarding the future of Amazon forest's carbon stocks are

103 contradictory and diverge both on the magnitude and on the direction of change (Huntingford

104 et al., 2013; Powell et al., 2013; Rammig et al., 2010). Different climate scenarios, process

105 formulations (e.g., nutrient limitations to CO_2 fertilization) and model parameterizations may

106 be some possible reasons for such uncertainties (Huntingford et al., 2013; Quillet, Peng, &

107 Garneau, 2010; Sitch et al., 2008; Verheijen et al., 2015). However,….

You could maybe have 1-2 sentences more about the projected decrease (and cite Hubau et al. 2020) and about the uncertainties (which uncertainties)?
User
03/15/2021 13:23

I also missed a brief review here (maybe one sentence or two) about the observed shifts in floristic and functional composition related to drought. Maybe the previously suggested articles can help …

https://onlinelibrary.wiley.com/doi/

https://www.nature.com/articles/s4

Bianca Rius
03/26/2021 10:12

Which question?
User
03/15/2021 13:25

Here it seems that a concluding remark or the connection to the next paragraph is missing…
User
03/15/2021 13:29

108 Additionally, the poor functional trait diversity represented in DGVMs in the tropics is

109 another feature that can potentially lead to inaccurate estimates of the impacts of

110 environmental changes on ecosystems, especially in hyperdiverse (at least in the taxonomic

111 sense) ecosystems such as the Amazon forest (Aguirre-Gutiérrez et al., 2019). This is because

112 it is reasonable to expect alterations in the environmental filtering following climatic changes,

113 and hence, the requirements for an individual to be successful may change as well (Webb,

114 Hoeting, Ames, Pyne, & LeRoy Poff, 2010). It implies that the physiological tolerances

115 determined by functional traits are also modified, possibly generating a rearrangement of the

116 community traits distribution (e.g., frequency and occurrence) and selection for alternative

117 functional structure, composition and diversity of the forest community (Enquist et al., 2015;

118 Thompson, Mackey, McNulty, & Mosseler, 2009; Wieczynski et al., 2019). Functional

119 diversity can be decomposed into the following components: richness, divergence and

120 evenness, all of which can respond differently to disturbances and thus play different roles

121 within emerging plant communities. As has been shown in some observational studies, the

122 rearrangement and modification of plant functional diversity components can affect the

123 forest's resilience to novel and unprecedented climatic conditions s (Aguirre-Gutiérrez et al.,

124 2019; Enquist & Enquist, 2011; Fauset et al., 2012, 2015; Wieczynski et al., 2019).

125 Currently The the ability of the majority of DGVMs to capture such plant community

126 rearrangement in vegetation models is very limited (Fyllas et al., 2014; Scheiter, Langan, &

127 Higgins, 2013) since they commonly DGVMs usually rely on the concept of plant functional

128 types (PFTs) to represent vegetation (Reu et al., 2014; Scheiter et al., 2013; Verheijen et al.,

129 2015). They represent vegetation by a very small, discrete, and *a priori* defined set of plant

130 types. Therefore, the diversity of plant functional strategies and associated functional

131 responses and the possibility for selecting alternative strategies that may deal better with the

> Instead of formulating it as a limitation, you could also say that DGVMs consider PFTs and their related strategies and that you now extend this approach.
>
> User
> 03/15/2021 13:37

132 new climate condition are limited (Fyllas et al., 2014; Mori, Furukawa, & Sasaki, 2013) and

133 thus hampers our understanding of yet unknown effects of climate change on plant functional

134 diversity and associated ecosystem processes driven by the emerging plant species community

135 (Díaz & Cabido, 2001; Lavorel & Garnier, 2002).

136 ~~In order to overcome these limitations that~~ a PFT approach imposes, some vegetation models

137 ~~- the so-called~~ Trait-based vegetation models represent plant trait diversity in a less discrete

138 manner (Fyllas et al., 2014; Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Sakschewski et

139 al., 2016; Scheiter et al., 2013) and replace the fixed parameters representing the functional

140 traits in PFTs by variable ones (Pavlick, Drewry, Bohn, Reu, & Kleidon, 2013; Reu et al.,

141 2014; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010; Wullschleger et al., 2014), thus

142 allowing a more flexible representation of plant functional responses to a given environmental

143 condition (Scheiter et al., 2013). It timely provides the opportunity for models to look beyond

144 biogeochemical variables creating potential for exploring a multiplicity of functional ecology-

145 related questions (Sakschewski et al., 2016; Darela-Filho et al., in prep.), many of them still

146 unexplored, such as the role of the different components of functional diversity on resilience

147 against environmental changes. Notwithstanding, the ability of trait-based models to

148 effectively capture the representation of ecological processes that are commonly considered in

149 standard DGVMs is yet to be assessed, as well as the comparative difference in the plant

150 functional response to environmental changes.

151 Here, we employed a vegetation model applied for the Amazon region in a scenario of

152 persisting drought. Two modeling approaches were used - one with low functional diversity

153 (PFT approach) and one with high functional diversity (trait-based approach) - to investigate

154 three main questions: (i) how do the modeling approaches differ in their results regarding the

155 Amazon forest capacity to absorb and store carbon under the drought scenario?; (ii) what is

6

Comments:

> If the effects are unknown, you won't be able to resolve them with trait-based modelling approaches either.
> User
> 03/15/2021 13:39

> But see our most recent article in Nature Plants and the upcoming paper in Ecology & Evolution (should you want to include some of these in the list of references):
>
> Franklin, O. , Harrison, S.P., Dewar, R., Farrior, C.E., Brännström, Å., Dieckmann, U. , Pietsch, S., Falster, S., et al. (2020). Organizing principles for vegetation dynamics. Nature Plants 6, 444-453. 10.1038/s41477-020-0655-x.
>
> Hofhansl, F., Chacón-Madrigal, E., Brännström, Å., Dieckmann, U., & Franklin, O. (2021). Mechanisms driving plant functional trait variation in a tropical forest. Ecology and Evolution (In Press)
> Florian Hofhansl
> 03/04/2021 15:42

> Maybe it might be even better to swap these research questions for specific research hypothesis, which could furthermore be used to structure respective paragraphs in the discussion section? This would improve the presentation of the different aspects and could be used to structure to the manuscript!
> Florian Hofhansl
> 03/05/2021 11:39

156 the drought impact on the different components of functional diversity for both modeling

157 approaches?; and, finally, (iii) what is the role of the functional diversity level and the

158 impacts of drought on it to the response of the two modeling approaches regarding the carbon

159 storage?

160 **Materials and methods**

161 *The CAETÊ model: an overview*

162 As a trait-based model, the CArbon and Ecosystem functional-Trait Evaluation (CAETÊ)

163 model focus on representing a higher variability of plant functional traits and, whenever

164 possible, the range of functional diversity found in plant communities. As such, vegetation is

165 represented by a set of functional strategies (hereafter called plant life strategies, PLS), each

166 of which refers to a unique combination of functional traits values. The combination of such

167 trait values describes the ecophysiological behavior of plants and their relationship with the

168 environment. These traits control, for example, the differential acquisition of carbon, light and

169 water, ultimately defining how the strategy copes with the environment and, together with the

170 other PLSs of the community, determine ecosystem functioning (Figure 1).

171 The underlying premise to create these PLSs is that the range of values of a functional trait

172 observed in nature can be regarded as one axis of a multidimensional hypervolume formed by

173 the combination of n chosen functional traits (Blonder, 2017; Villéger, Mason, & Mouillot,

174 2008). In that sense, each point inside of this hypervolume is a unique combination of values

175 for each of the functional traits, a PLS. The volume that all points together occupy can be seen

176 as a functional trait space. The values of functional traits that compose the hypervolume are

177 semi-randomly sampled from the complete range of values (for more details see Appendix

178 A.1). The combination of all sampled values generates a large number ($>10^5$) of combinations

7

This figure is really great and gives a good overview of the diferente approaches, however, some of the other figures I found quite difficult to read/understand.
Florian Hofhansl
03/05/2021 11:46

Necessário rever essas referencias

Bianca Rius
03/19/2021 16:50

179   within the functional space. Similar to other trait-based models (e.g., Pavlick, Drewry, Bohn,

180   Reu, & Kleidon, 2013; Reu et al., 2011), CAETÊ follows the assumption that sampling an

181   appropriate number of PLSs from the potential functional space (see sensitivity test in

182   Appendix A.2) combined with an environmental filtering mechanism together with a

183   representation of competition allow the model to produce reasonable biogeochemical and

184   functional diversity patterns.

185   The environmental filtering mechanism acts in the model such that each PLS within the trait

186   space performs differently under the same environmental conditions such as temperature and

187   precipitation; Diaz, Cabido, & Casanoves, 1998; Webb et al., 2010). All grid cells are

188   initiated with the same set of PLSs (number and identity) in a condition analogous to a bare

189   soil. Therefore, even though all trait combinations are equally probable to occupy a given grid

190   cell , it is expected that some PLSs will survive and present different performances and

191   abundances and some of them will perish in the simulation. PLSs that do not survive are

192   excluded from the grid cell (and cannot be reestablished in that grid cell in this model

193   version).

194   The differential survival and abundance between PLSs are made possible because each

195   functional trait in the model is related to at least one trade-off (cost-benefit relationship)

196   leading to different relative performances and ability to deal with the environment. The trade-

197   offs also prevent the model from creating the so-called "Darwinian demons" (i.e., maximizing

198   all the functions that contribute for fitness; Scheiter et al., 2013). Since functional traits both

199   respond to and affect ecosystem-level processes (Díaz et al., 2013; Funk et al., 2017; Lavorel

200   & Garnier, 2002) the varying PLSs ecophysiological performance generates heterogeneous

201   biogeochemical fluxes and stocks and functional diversity through space and time. Such

202   model outputs are aggregated to the grid cell scale according to the modeled abundances of

I think it is important to briefly describe the trade-offs here and also maybe it would be interesting to give more focus on the relation of such trade-offs to the obtained results in the discussion section.
Bianca Rius
03/26/2021 10:14

203 PLSs, which are determined on the basis of the biomass-ratio hypothesis (Grime, 1998; see

204 Appendix XXX). The ecophysiological processes linked to each functional trait, its trade-offs,

205 and associated formulations are summarized in Table A.3 and described in Appendix A.3.2.

206 An in-depth description of the CAETÊ model can be found in Appendix A.3.

207 *Simulation setup*

208 In this study we employed, for the Amazon basin, a non-dynamic version of the CAETÊ

209 model, which calculates equilibrium solutions based on long-term mean monthly climate

210 variables (for the period between 1980 and 2010; see Appendix XX). A spinup simulation

211 period of ????? years was carried out to initialize carbon stocks in different plant

212 compartments (see Appendix A.3.4).

213 Two sets of model runs were carried out: one employing, as the majority of current vegetation

214 models, a PFT approach (with a low functional diversity initialization: 3 PFTs) and the other

215 using a trait-based approach (with a high functional diversity initialization: 3000 PLSs).

216 Despite the difference in the number of plant types and in the way that functional traits values

217 are chosen, the general model formulations and principles are the same for both approaches.

218   We set six functional traits to be variable between PLSs/PFTs; since our focus of analysis

219 here is on the process of carbon storage three of them regard the percentage of the carbon

220 distributed to different plant compartments (i.e. carbon allocation to leaves, roots and

221 aboveground woody tissues (hereafter ABGW)) and the other three traits represent carbon

222 residence time - how long the carbon remains - in each one of the plant compartments above

223 cited. Together, these functional traits ultimately define the amount of carbon in each plant

224 tissue of a PLS or PFT at each time step, and are of primary importance for determining

9

Will you have all tables related to the simulations and methods in the appendix? it could be helpful to include a figure that describes the model versions, simulations, etc. KF
Bianca Rius
03/29/2021 16:17

João, can you help me with this number
?
Bianca Rius
01/29/2020 00:53

refer to table with parameters for PFTs, and ranges of parameters for trait-based approach KF
Bianca Rius
03/29/2021 16:11

usually aboveground gets AG but lately I have seen ABG but this seems really long. check if their are common terms elsewhere. ABGW is not so pretty. Do you really need it? KF
Bianca Rius
03/29/2021 16:12

that last sentences sounds a bit awkward.

I feel you state a little too strongly that you focus on "the process of carbon storage" - it is about the processes that in combination lead to carbon storage in the ecosystem, so you focus on a number of key processes that control carbon storage and the response to climate change, drought, right? KF
Bianca Rius
03/29/2021 16:14

Responder a Bianca Rius (03/29/2021, 16:14): "..."
Carbono como variável de estado?
Bianca Rius
03/29/2021 16:14

225 absorption and storage of carbon in the study system (Chambers, Fisher, Hall, Norby, &

226 Wofsy, 2012; Fatichi & Leuzinger, 2013; Malhi, 2012; Norby et al., 2005).

227 Three tropical PFTs were defined in the PFTA to describe the vegetation and the parameters

228 that represent the functional traits used for this study are *a priori* defined following previous

229 literature (Table A.1). ~~The use of only tropical PFTs is justified given the study region~~

230 ~~(Amazon forest), and with them,~~ we tried to encompass the majority of PFTs previously used

231 in standard DGVMs. In the trait-based model approach, the initial range of values for each

232 functional trait considered as variable (from where some of them will be sampled to create the

233 hypervolume) are indicated in Table A.2. It is important to highlight that CAETÊ admits the

234 use of any functional trait of interest, as well as any number of them, as long as the trait is

235 linked to existing model formulation and can have trade-offs implemented. CAETÊ works at

236 a spatial resolution of 0.5º x 0.5º and is coded mainly in Fortran 90 with some modules

237 written in Python.

238 *Input data*

239 The following climatic data were used as inputs for the model: air surface temperature,

240 precipitation, shortwave radiation, relative humidity and atmospheric CO_2 concentration. The

241 first four variables were obtained from mean monthly data for the period between 1980 to

242 2010. which are available in the Inter-Sectoral Impact Model Intercomparison Project 2 (ISI-

243 MIP2; Warszawski et al., 2014). Atmospheric CO_2 concentration was obtained from the

244 National   Oceanic   and   Atmospheric   Administration   platform

245 (http://co2now.org/images/stories/data/co2-mlo-monthly-noaa-esrl.pdf), using the mean value

246 of [CO_2] for the same period of the others climatic data..

247 *Representation of functional diversity and composition*

248 Here we focused on a large-scale analysis of functional diversity for the whole Amazon basin,

249 in opposition to a detailed grid cell-by-grid cell analysis. In that sense, the value of each of the

250 six variant functional traits in each grid cell is represented by a mean value that is estimated

251 according to the relative abundances of PFT/PLSs (see Appendix A.3.1) using the

252 Community Weighted Mean (CWM) metric (Díaz et al., 2007; Grime, 1998).

253 Additionally, functional diversity is regarded here both from the perspective of its single-trait

254 components as well as its multi-trait component (i.e., the combination of traits). The single-

255 trait element allows to interpret more precisely how the different traits interact (affects and

256 responds) with the environment (Lepš, de Bello, Lavorel, & Berman, 2006; Ricotta &

257 Moretti, 2011), while the multi-trait component gives information about the ecological

258 strategy as a whole (i.e., as a coordinated trait syndrome), thus accounting for the

259 coordination of traits, including its trade-offs, and also how the community occupies the given

260 possible functional space (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016;

261 Blonder, Lamanna, Violle, & Enquist, 2014).

262 Following the definitions and methods by Carmona et al. (2016) we considered that single-

263 trait functional diversity can be decomposed into three components: (i) functional richness:

264 the portion of the total functional trait space, i.e, the total range of values for a specific

265 functional trait, that is occupied in an ecological unit derived from the variance of trait values

266 of all the considered organisms (PFT/PLSs in our case); (ii) functional evenness: the

267 regularity of the density distribution of the PLSs' or PFTs' trait values in the functional trait

268 space; (iii) functional divergence: the degree to which the abundance of PFT/PLSs' trait

269 values are distributed towards the extremes of their functional trait space. Carmona's method

270 uses probability density distributions for the calculation of the components, the so-called

271 TPDs (trait probability distributions).

I dont understand this first sentence? what do you mean by "grid-by'grid"analysis?

I think it can go out, now that I read the next sentences, its fine to only say use mean value per grid.
KF
Bianca Rius
03/29/2021 16:21

272 For multi-trait functional diversity, we used the hypervolume metric following Blonder et al.

273 (2014). Hypervolumes can combine the distribution of *n* trait values and then calculate

274 functional diversity components (Barros et al., 2016; Blonder et al., 2018), for example, the

275 volume size, that indicates how much of the possible functional space an ecological unit

276 occupies (i.e., the variance of values; Barros et al., 2016), that can be interpreted as functional

277 richness. Also, the distribution of values within the hypervolume informs, together with the

278 centroid (that indicates the mean values), about system functional composition.

279 As recommended by Barros et al. (2016) we performed a principal component analysis (PCA)

280 with a centered and scaled method (see Figure SM.1.). PCA was also necessary because our

281 traits are correlated (e.g. the allocation for one –is correlated to the allocation in the others)

282 and, it was also necessary in order to reduce the number of variables (six), which exceeded

283 the maximum number of variables for constructing the hypervolume in the used metric

284 (Blonder et al., 2014). Then, the PCA allows the delineation of the hypervolume using the

285 factor scores of the chosen PC's. Additionally, the PCA indicates the trade-offs that emerge

286 from the model results. All the analyses were performed in the R platform. We used the

287 package *TPD* (Carmona, 2019) for the analysis of single-trait functional diversity, the

288 package *hypervolume* (Blonder, 2019) for the analysis of multi-trait functional diversity, and

289 the function *prcomp* of the package *stats v3.6.2* (R core team, 2013) for the PCA.

290 *The role of functional diversity on ecosystem response to environmental change*

291 To test the potential effects of functional diversity on the ecosystem's biogeochemical

292 response to drought, we applied a homogeneous reduction of 50% on precipitation for the

293 whole Amazon basin. In this model application we were interested in testing if a plant

294 community with higher functional diversity (trait-based approach) responded differently to a

12

Margin comments:

Probably you would have to indicate some additional details, such as rotation of axis and number of componentes used, as well as what criterion (e.g., Kaiser) has been used to select the number of axis?!
Florian Hofhansl
03/05/2021 12:06

delete what is in bracktes here, no need
KF
Bianca Rius
03/29/2021 16:21

is the title suitable here? I am not sure about the meaning of this section actually, seems like it basically says that you will analyse the affect of drought on carbon storage - and there is info on general aims and the sims in here
KF
Bianca Rius
03/29/2021 16:22

better to avoid starting sentences with "To"
KF
Bianca Rius
03/29/2021 16:23

Here and elsewhere when you use the term "drought". Make sure that you explain here that you do a "stylized scenario" or "hypothetical drought" or something like that. Otherwise you might get some critiques that what you are doing is not climatologically consistent etc.
User
03/15/2021 16:48

What do you mean with homogeneous reduction of 50%? Each month? Over the year? In the rainy season? For which time period? This should be explained.
User
03/15/2021 16:42

drier climate in its ability to store and partition carbon compared to a community with lower functional diversity (PFT approach). For this we compared the degree of change in carbon stock either considering the whole plant or the compartments separately. To complement this analysis, we explored the underlying mechanisms generating the difference ~~of response by exploring the effects of drought on~~ in the observed functional community metrics ~~diversity and composition~~ *per se* (see next section).

Functional composition and diversity response to drought

For the single-trait framework analysis, we compared the TPDs generated by the two climatic conditions for all the six traits: regular climate and reduced precipitation. For this, the dissimilarities between the two TPDs 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 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 framework four hypervolumes were constructed and compared: using regular climate condition and using reduced precipitation for each of the modeling approaches. After performing the PCA (a previous necessary step explained in section *Representation of functional diversity and composition*) the hypervolumes were delineated using the factor scores of the three first principal components (PCs) since they were able to explain more than 98% of the variance. It is important to highlight that we needed to calculate the PCA with both climatic conditions and for the two modeling approaches together (Barros

13

318 et al., 2016); after that, separate hypervolumes were calculated from the factor scores

319 corresponding to each climatic condition and model approach dataset. After constructing the

320 four hypervolumes we were able to compare them in terms of size (richness), the distance

321 between the centroids (to verify the change in mean values) and the degree of overlap through

322 Jaccard similarity index that range from 0 (completely dissimilar) to 1 (completely similar).

323 These three metrics together indicate the magnitude of change in functional diversity and

324 composition in response to a drier climate considering different plant ecological strategies.

Results

Drought impacts on carbon storage and partitioning

327 The 50% reduction of precipitation caused a considerable basin-wide reduction of carbon

328 stocks both for the high and low degrees of functional diversity employed in the model: -

329 57.48% and -57.45%, respectively. Also, for both approaches the reduction was higher in

330 regions with naturally lower precipitation levels, mainly in southern, central and northern

331 parts of the basin (Figure 2a and 2b). However, the spatial pattern of carbon loss driven by the

332 imposed drought condition differs between the trait-based (hereafter TBA) and PFT

333 approaches (hereafter PFTA). The TBA was able to maintain carbon stocks in some areas

334 where in PFTA carbon stocks were completely lost. This is more evident in naturally drier

335 areas, such as the transition between the Amazon forest and the savannah (*cerrado*) and

336 central Amazon. It is noteworthy also that the loss of carbon in TBA is more gradual, i.e.,

337 there is a smoother gradient between a grid cell value and its neighboring cells, and also

338 across different basin regions. On the other hand, in the PFTA the carbon loss is more abrupt

339 both between neighboring cells and across the regions of the basin.

Margin comments:

not sure what you mean with "considering plant ecological strategies as a whole"?
KF
Bianca Rius
03/29/2021 16:27

it is a little weird that the number are so precise and so similar. Perhaps both 57.5% is enough? or even 57%
KF
Bianca Rius
03/30/2021 12:03

This reduction was ... for both approaches.
kf
Bianca Rius
03/30/2021 12:05

and bring this sentence after the next one. First say spatial patterns differ, then explain how.
Kf
Bianca Rius
03/30/2021 12:06

has lost it completely? zero carbon?
KF
Bianca Rius
03/30/2021 12:08

that is an interesting result!
Bianca Rius
03/30/2021 12:08

340 Despite the similar magnitude in the total carbon storage change, specific plant compartments

341 have shown different patterns of changes when comparing the two approaches (Figure 2c and

342 2d for fine roots and Figure SM.2 for leaves and ABGW). None of the compartments has

343 shown, for any area, an increase in carbon stock with drought, except for the fine roots

344 compartment in TBA, indicating a change in carbon partitioning for the latter approach. This

345 increase, around 10% (blue areas in Figure 2d), was observed in the transitions from humid

346 and evergreen forest to the Brazilian savannahs (*cerrado*) and also in the basin northwest.

347 Even in areas where the root compartment has lost carbon in the TBA, it was to a lower

348 degree when compared to the other compartments and to the PFTA approach.

349 *Functional composition under reduced precipitation~~a drier climate~~*

350 The applied drought scenario caused a modification in the density distribution of the six

351 variant functional traits both for PFTA and for TBA (Figure 3). For all the traits, the shape of

352 the curve changed considerably, (i.e., the dissimilarity index approximating to 1), which

353 indicates that they became functionally different with the new climatic condition (Table 1).

354 For example for all of them, the maximum values of the probability density distributions were

355 lower under low precipitation, that is, the peak of the curves decreased, meaning that there

356 was a clear and strong reduction in dominance for the communities under drought. Because of

357 the observed decrease in dominance other trait values that were previously rare (very low

358 density), or absent, were able to co-occur in the trait space or to increase their density,

359 changing the shape of the curves, which ultimately demonstrates a change in the functional

360 composition of the communities and in the different components of functional diversity.

361 Nevertheless, the change in functional composition was different when comparing the

362 modeling approaches. First, considering all the traits, the PFTA showed a trimodal

15

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 (Figure 4a), and

a much less discretized data distribution from the TBA (Figure 4b). Also, for the TBA it is

important to observe that the increase in the trait values density is more prominent for the

ones that were previously rare under the regular climate conditions (Figure 3a-c and g-i). In

that sense, the TBA showed a clear pattern with reduction in precipitation for traits related to

carbon allocation: an increase in density toward higher values of carbon in fine roots and an

increase in density toward lower values of carbon in leaves and especially in ABGW. On the

other hand, the PFTA showed a much smaller change, and changes in density values were

restricted to a small area of the functional space, with almost no change in the range of values

(Figure 3d-f and j-l). A similar pattern of density distribution change was found for traits

related to residence time: the PFTA showed an increase in residence time for leaves and fine

roots (despite the very slight change) and a conservation in residence time values for ABGW

(Figure 3j-l), while for TBA we observed an increase in residence time for leaves and fine

roots but a decrease for ABGW (Figure 3g-i).

Functional diversity under drought scenario

The above-cited changes drove alterations in the three facets of functional diversity within the

two employed modeling approaches (Figure 5). In general, we found an increase in functional

richness for all traits in both approaches, but the percentage of change in this facet was much

higher in TBA. Functional evenness showed an increase superior to 100% in TBA,

nonetheless, in the PFTA traits showed a decrease in this functional diversity component and

16

387   in a lower degree of change (74% maximum). As a whole, the TBA traits presented reduction

388   in divergence, while the opposite result was observed for the PFTA, also with the same

389   pattern found for the other functional diversity facets regarding the magnitude of change.

390   Also, with the applied drought scenario, the hypervolumes for TBA and PFTA showed a

391   pronounced change. (Figure 4; see movie SM.1 for a 3D animated representation). Under

392   natural climatic conditions the size of the volume that the data occupy was equal to 1.711 and

393   0.007 for TBA and PFTA, respectively; while under reduced precipitation the volume size

394   increased for both approaches: 47.837 for the former and 0.755 for the latter. It indicates an

395   increase in the occupation fraction of the functional space under a drier climate (i.e., increase

396   in the amplitude of trait's variation and richness) in a magnitude of 2,695.0% for the TBA and

397   1,025.0% for the PFTA. The overlap degree between hypervolumes (before and after the

398   drought scenario) yielded a value of 0.038 for the TBA and of 0.009 for the PFTA, indicating

399   almost no similarity of the hypervolumes. Finally, the distance between the centroids of the

400   two hypervolumes after imposing a climatic change indicated a change in the mean values:

401   the centroid distance for the TBA was 5.25 and 0.937 for the PFTA, that is, the mean values

402   were modified to a higher magnitude for the former approach.

403   **Discussion**

404   Briefly, our results showed: (i) PFTA and TBA approaches presented a similar magnitude

405   decrease in total carbon storage capacity in response to precipitation reduction; (ii) the

406   changes along the basin was much more smoother for TBA than for PFTA, with the former

407   presenting carbon stock conservation in grid-cells where the latter was not able to; (iii) all the

408   plant compartments showed a reduction in storing carbon, except for an fine roots in TBA

409   that presented an increase of investment in this tissue; (iv) both modeling approaches

presented changes on the three facets of functional diversity, however the magnitude of the change was much higher in TBA; (v) functional diversity modifications derived from a functional reorganization of communities, but because of the smaller diversity of possible combinations (3 PFTs), this reorganization for PFTA was less conspicuous.

Ecological mechanisms

As expected, the 50% reduction in precipitation caused a pervasive decrease (~60%) in the basin carbon stock for both modeling approaches, concentrated mainly in naturally drier regions. This massive decrease of Amazon forest ability to store carbon in drought 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.

However, we expected a more pronounced difference between the TBA and PFTA since it is widely accepted that a more diverse (both taxonomically and functionally speaking) ecosystem tends to be more resilient to environmental changes (Cadotte, Carscadden, & Mirotchnick, 2011; Mori et al., 2013; Sakschewski et al., 2016; Schmitt et al., 2019). However, the similar C loss magnitude can be partially explained by the fact that the carbon assimilation processes (photosynthesis and respiration) were not modified between the two modelling approaches and some important processes such as embolism and functional traits

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Margin comments:

that last bullet point is trying to make that point I was missing in the bullet point above, but a little too complicated..
kf
Bianca Rius
03/30/2021 12:30

ecological mechanisms underlying carbon responses to drought
kf
Bianca Rius
03/30/2021 12:30

Wouldn't you rather expect that carbon losses are larger in naturally not so dry regions because forests are not so well adapted to drought?
User
03/15/2021 17:12

I wonder whether it would be possible to relate your 60% number a bit more? previous studies would also give drought impact results in terms of Pg C stored, or % complete dieback, etc.

saying that 60% reduction is i agreement with so many different studies is not nuanced enough.
Kf
Bianca Rius
03/30/2021 15:06

so through carbon starvation speaking in drought-people language ;)
kf
Bianca Rius
03/30/2021 15:06

This could be used as a hypothesis at the end of the introduction section!
Florian Hofhansl
03/05/2021 13:53

so through carbon starvation speaking in drought-people language ;)
Bianca Rius
03/30/2021 15:07

not sure this explanation satisfies me.

if plants have less carbon available will they then not benefit from different allocation patterns?
Bianca Rius
03/30/2021 15:07

432 linked to drought response are still not included in the model (in the *Discussion* section some

433 caveats are presented).

434 Nevertheless, despite the similar magnitude in total carbon loss, the two approaches presented

435 differences in the spatial pattern: the model approach with high initial functional diversity

436 (TBA) was able to maintain carbon in regions where the other approach with low initial

437 functional diversity (PFTA) lost it completely, especially in the southern and central parts of

438 the Amazon forest, even though the former lost carbon to a higher degree than the second

439 where both modeling approaches maintained carbon. This result at first may seem

440 contradictory but can be explained by the fact that the underlying mechanisms accounting for

441 ecosystem carbon storage was different between the modelling approaches: while the PFTA

442 showed, on average, almost no change in the carbon partitioning with drought, the TBA

443 increased the investment in fine roots by a trade-off in the relative investment to leaves and

444 ABGW. It is well known that climatic changes, such as drought, induce changes on C

445 partitioning patterns (Doughty et al., 2014; Kannenberg et al., 2019) including a prioritization

446 of root investment at the expense of other tissues (Doughty et al., 2014; Phillips et al., 2016;

447 Rowland et al., 2014). In our model, a higher investment in fine roots increases the uptake of

448 water, which makes the community better able to deal with drought and maintain carbon

449 stocks or reduce the degree of loss. We observed it in the TBA: an avoided of total carbon

450 loss in grid cells where the PFTA was not able to hold it. This happened because the TBA

451 could make a carbon investment rearrangement while the PFTA could not (the discussion of

452 the reason is presented in the next section).

453 The shift in carbon partitioning due to climate is of primary relevance for the future of

454 Amazon carbon stocks (Doughty et al., 2015; Friedlingstein et al., 2006) and is especially

455 important if the carbon is allocated towards pools with shorter turnover, such as fine roots or

19

456 even root exudates (Jiang et al., 2020), that contribute to a lesser extent to total carbon storage

457 comparatively with other pools such as wood tissues (Chave et al., 2009; De Kauwe et al.,

458 2014; Kannenberg et al., 2019; Luo, 2003). Our modeling exercise captured well this process:

459 the drought triggered an increase in investment of fine roots in the TBA that provided greater

460 resistance to drought, preventing the total loss of carbon in several grid-cells, and also caused

461 a lower carbon storage in other tissues, mainly on ABGW and led to a relative lower carbon

462 storage in some locations when compared to the PFTA. In that sense, if the ability to store

463 carbon is used as the only proxy for ecosystem resilience, as is commonly used, (e.g.,

464 Sakschewski et al. 2016; Huntingford et al., 2013; Levine et al., 2016), it may result in

465 inaccurate interpretations about the response of tropical forests to climate change.

> **Comment (Bianca Rius, 03/30/2021 15:09):** not sure what you mean here? usually AG wood is the proxy for resilience I would say

466 Lastly, since model formulation was equal in the two approaches, one can conclude that the

467 differences observed regarding carbon storage are derived from the ~~initial~~ difference in (a) the

468 functional <u>characterization of the plant community and (b) the allocation of carbon to</u>

469 <u>different plant tissues, both of which affect the residence time of carbon in the system</u>~~diversity~~

470 ~~employed and from the changes that the imposed climatic scenario caused on different~~

471 ~~components of functional diversity~~.

Forest functional reorganization

473 Our results show that the applied long-term precipitation reduction scenario caused a

474 significant functional community reorganization of Amazon forest in terms of composition,

475 dominance relationship, functional richness, evenness and divergence both for the PFTA and

476 TBA. The functional reorganization is supported by the dissimilarity values found between

477 traits distributions before and after the disturbance both in the single-trait and multi-trait

478 analysis.

> **Comment (Bianca Rius, 03/30/2021 15:12):** that is a nice sentence! more of these

479 These results are in agreement with theoretical, experimental and modeling evidences that

480 show environmental change is able to cause a modification on functional structure (Enquist &

481 Enquist, 2011; Hillebrand, Bennett, & Cadotte, 2008; Mouillot, Villéger, Scherer-Lorenzen,

482 & Mason, 2011), dominance (Hillebrand et al., 2008; Schmitt et al., 2019; Valencia et al.,

483 2015), composition (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2018; Nepstad,

484 Tohver, Ray, Moutinho, & Cardinot, 2007) and diversity components (Hillebrand et al., 2008;

485 Zhang, Chen, & Reich, 2012). In our simulations these changes occurred because the

486 environmental filtering was modified and, as a consequence, the selection of the strategies

487 changed towards favoring trait values that were previously rare or absent. Those changes

488 modified the abundance of traits and the way that communities occupy the functional space

489 (Carmona, de Bello, Mason, & Lepš, 2016, 2019; De Bello, Carmona, Mason, Sebastià, &

490 Lepš, 2013; Enquist & Enquist, 2011). Next sections explore the changes related to functional

491 dominance, composition and diversity components.

492 *Changing functional dominance*

493 The differential occupation of the functional space with drought was specially caused by the

494 change in dominance: an expressive decrease in abundance of a narrow range of trait values to

495 a wider one for all the considered traits, especially for the TBA. Dominance reflects the

496 distribution of traits in a community and plays a fundamental role on ecosystem processes,

497 such as carbon cycling (Cavanaugh et al., 2014; Ruiz-Jaen & Potvin, 2011), since,

498 theoretically, the dominant traits contribute more to aggregate processes in communities and

499 ecosystems when compared to rare ones (Hillebrand et al., 2008).

500 The dominance change modeled in our study and observed/theorized in the other studies cited

501 above, is in agreement with the theory that the shift in community dominance with a change

21

in climate could be caused by a compensatory dynamic process, also called as 'functional density compensation': when the composition of an ecosystem 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). As a consequence, the diversity of trait values available in a community is central, since it can act as an "insurance" for new environmental conditions (Fauset et al., 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016; Yachi & Loreau, 1999). It also reinforces the importance of rare trait values, functional strategies or species, for the maintenance of ecosystem processes in future environmental conditions, including tropical forests that commonly present a hyperdominance of species with specific functional traits (Cornwell, Schwilk, & Ackerly, 2006; Jain et al., 2014; Mouillot et al., 2013; van der Sande et al., 2017).

Such a functional density compensation phenomenon was well captured in our modeling results: reduced precipitation led to a consequent emergence of new strategies and/or increase in abundance of previously rare trait values occurrence. However, the capacity of a community to promote compensatory dynamics strongly depends on its functional diversity (Mori et al., 2013). This was clearly demonstrated in our work when comparing the PFTA and the TBA. The functional space occupation as a consequence of the decrease in dominance was different for the approaches, for example, the PFTA presented, for all traits, a restricted probability of the occurrence of new trait values, presenting trimodal curves with drought. On the other hand, the trait-based approach showed a more widespread occupation of the functional space. 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.

Margin comments:

nice! bring this straight away - KF
Bianca Rius 03/30/2021 15:16

try and go more clearly to the point when discussing aspects of your analysis - avoid too much summarizing what was said in the results before
Bianca Rius 03/30/2021 15:17

We found this pattern also for neotropical forests in our study region in Costa Rica:

Morera-Beita, A., Sánchez, D., Wanek, W., Hofhansl, F., Werner, H., Chacón-Madrigal, E., Montero-Muñoz, J.L., & Silla, F. (2019). Beta diversity and oligarchic dominance in the tropical forests of Southern Costa Rica. Biotropica 51 (2), 117-128. 10.1111/btp.12638.
Florian Hofhansl 03/04/2021 16:07

like here - there is no need to explain this again.. the sentence before "the capacity./..... depends on functional diversirty"this is the point, "demonstrated between PFTA and TBA approach" - keep it simple and clear.
Bianca Rius 03/30/2021 15:18

526   These contrasting results are due to the modeling approach-dependent difference in the

527   diversity of responses that traits or trait combinations show to disturbances in a given

528   community (Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016) that was imposed by

529   the level of functional diversity in which the model was initialized. Such a response diversity

530   was very limited for the PFTA since it was provided with only 3 possibilities of trait

531   combinations, preventing better suited traits combination to establish themselves under the

532   new climatic conditions whereas the TBA was provided with 3000 possible trait

533   combinations. It also explains why the carbon partitioning rearrangement was so relatively

534   more limited for the PFTA.

535   Also, the different diversity of responses within the approaches can explain the spatial

536   difference observed in vegetation carbon storage. The smoother pattern of carbon loss

537   observed in the TBA was possible because of its higher capacity of functional reorganization

538   due to response diversity, selecting better suited trait combinations in accordance with the

539   grid-cell environment. Meanwhile, the PFTA presents a reorganization very restricted because

540   of its low diversity of responses and the change of environmental conditions between one grid

541   cell and another could not be suitable for the 3 available trait combinations.

542   *Changing functional composition*

543   In the present study the different employed modeling approaches presented distinct responses

544   in terms of changes in community composition, which are mainly associated to the magnitude

545   of the change: while the change in the occupation of the functional space for the TBA showed

546   a prominent shift in allocation towards fine roots, in the PFTA the composition change is

547   much less remarkable, with the maintenance of the more abundant traits around the same

548   range of values prior to the imposed climatic change. That means the TBA was able to select

549   strategies that coped better with the drought scenario by increasing fine roots allocation and

23

550 residence time, since this tissue is strictly related to the water uptake; likewise, the increase

551 observed in residence time for leaves in this employed approach, despite the decrease in

552 allocation, can be identified as a mechanism to maintain the levels of photosynthesis since the

553 reduction of allocation for this organ reduces total photosynthetic rates for a given plant

554 strategy.

555 In fact, literature shows that carbon partitioning can exhibit plasticity depending on water

556 availability (Bazzaz, 1991; Franklin et al., 2012; Weiher et al., 1999; Weiner, 2004).

557 According to the optimal partitioning theory, the preferential allocation should be directed

558 towards the organ responsible for the acquisition of the most limited resource, in that sense,

559 one should expect, as observed in the TBA results, an increase towards roots investment under

560 water limitation (Cannell & Dewar, 1994; Metcalfe et al., 2010; Thornley, 1972). However,

561 the fate of carbon under drought conditions is still a matter of debate, and conflicting results

562 are found in the literature (Hofhansl, Schnecker, Singer, & Wanek, 2015; Litton, Raich, &

563 Ryan, 2007) but some pattern can be identified: apparently a mild drought, or stronger dry

564 seasons, lead to a higher investment in fine roots (Blessing, Werner, Siegwolf, & Buchmann,

565 2015; Brando et al., 2008; Doughty et al., 2014; Lacointe, 2000; Rowland et al., 2014), while

566 a more persistent and severe drought could decrease allocation belowground followed by a

567 higher investment in wood and canopy tissues (Blessing et al., 2015; Sevanto & Dickman,

568 2015). The investment in wood tissues could be explained by the fact that these organs

569 maximize plant hydraulic safety (Hofhansl et al., 2015).

570 In that sense, it seems that the impact of drought on allocation is not straightforward and may

571 depend on a series of variants that goes beyond carbon partitioning such as the duration,

572 severity of drought and other plants features like the sensitive to embolism and cavitation, not

573 yet addressed in the employed model formulation.

Margin comments:

that seems to be also more suitable above in the ecological mechanisms section KF
Bianca Rius
03/30/2021 15:20

sounds more suitable for the introduction
Bianca Rius
03/30/2021 15:21

This could be used for one of the hypothesis stated at the end of the introduction section!
Florian Hofhansl
03/04/2021 16:18

It would be interesting to know which "conflicting results" you are adressing here with our reference ;-)
Florian Hofhansl
03/05/2021 15:01

that is a nice discussion and differentiates, I wonder (after reading Flo's comments too) whether some of this should come earlier to help you formulate a hypothesis and here discuss why and how your model results support one or the other previous study. You should really focus on …
Bianca Rius
03/30/2021 15:22

I am not sure this is the right reference for such a statement, but would rather expect a reference to the studies by Rowland et al.:

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., …
Florian Hofhansl
03/05/2021 15:03

574 Comparing our results about the change in functional composition with other studies can be

575 tricky, once the result of studies regarding changes in functional composition is highly

576 dependent on the chosen traits. For example, Esquivel-Muelbert et al., (2018) and Aguirre-

577 Gutiérrez also found an increase in abundance of plants of the trait values of which confers

578 them a higher tolerance to drought. Despite of this obstacle in comparing the results, it is

579 obvious that our employed TBA was able to at least identify this type of community level

580 response, and thus provides a promising next step to include hydraulic, leaf and wood traits

581 that have been found crucial for depicting the response of ecosystems to drought (Barros et

582 al., 2019; Christoffersen et al., 2016; O. L. Phillips et al., 2010; Poorter et al., 2010). Our

583 findings related to functional traits composition become fundamental by allowing advances on

584 the still undergoing question of how functional shifts moderate drought-induced biomass loss

585 and forest resilience to environmental change.

586 *Functional diversity facets responses*

587 Few studies have explored how drought impacts the different functional diversity components

588 (Carmona, de Bello, Mason, & Lepš, 2016), despite the known importance of them for

589 ecosystem functioning and resilience (Carmona et al., 2016). Here we explored, for the first

590 time, the impact of drought on Amazon functional diversity considering its three primary

591 components: richness, evenness and divergence, and also examined functional diversity

592 considering all the six chosen functional traits together.

593 The observed impacts on functional diversity, for both modeling approaches, reflect a

594 functional reorganization of the plant community, especially with regard to the dominance

595 change. For functional richness we observed an increase in this variable for TBA and PFTA.

596 but the magnitude of change was much higher for the TBA, which might be due to the fact

This paragraph could be restructured to highlight one of the hypothesis proposed at the end of the introduction section, i.e., a more diverse system should be more resilient to environmental change.
Florian Hofhansl
03/05/2021 15:25

25

that the latter presents a wider range of possible values to occupy the functional space, while this range is very limited for the former. It also reflected on the volume occupied in the functional space considering the traits altogether: volume increases in both the approaches, but the TBA showed an increase more than two-fold stronger when compared to the PFTA. This is contrary to the hypothesis that a harsher environment would decrease functional richness by selecting a narrow range of strategies due to environmental filtering (Cornwell et al., 2006; Funk et al., 2017; Kleidon, Adams, Pavlick, & Reu, 2009; Perronne & Gaba, 2017). However, the observed functional reorganization is able to explain this unexpected result, since they allowed new combinations of traits to establish or increase their occurrence (Mouillot et al., 2013). It means that, in some cases, functional richness can increase in disturbance scenarios if the environmental change affects mainly the dominant strategies or trait values.

Regarding evenness: the increasing evenness in the six functional traits observed for the TBA means that the drought scenario made the distribution of trait values in the trait space to become more regular. 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.,

26

621 2017; Hillebrand et al., 2008; Mason, Mouillot, Lee, & Wilson, 2005; Mouillot et al., 2011).

622 Therefore, our results indicate that a change in the environment can force the community to

623 better occupy the functional niche space, if it presents a sufficient variability in its trait values,

624 as we observed for the TBA.

625 Lastly, the TBA presented a general decrease in divergence while the PFTA approach showed

626 an increase for this functional diversity facet. The decrease in divergence found for TBA

627 means that, regarding a specific trait, the values distribution is no longer concentrated in only

628 one extremity of the functional space, but other trait values that were not that important before

629 became significant for the community and for the ecosystem functioning with the

630 environmental change. Beyond that, divergence is also a way to understand if the frequency

631 distribution of trait values in the functional niche space maximizes the total community

632 variation in functional characters (Mason et al., 2005). In that sense, low divergence could be

633 a result of different, or even contrasting, strategies being able to deal with the new conditions

634 (Funk et al., 2017). The increase in divergence found in the PFTA is a product of the

635 emergence of the three peaks on traits distribution. For this approach a better occupation of

636 functional space (low divergence) is impossible considering its very low diversity of trait

637 values available.

638 *Conclusions*

639 In this study we aimed to explore the role of functional diversity on the ability of the Amazon

640 forest to store carbon under a persistent drought scenario (50% homogeneous precipitation

641 reduction). We employed the vegetation model CAETÊ with two levels of initial functional

642 diversity (low and high, PFT and trait-based respectively). In order to understand the

643 underlying mechanisms driving the observed responses of each approach, we evaluated the

27

644 connection of these results with different functional diversity components: composition,

645 dominance, richness, divergence and evenness.

646 We showed that the inclusion of a higher degree of functional diversity through the usage of a

647 trait-based approach plays a paramount role in the response of communities to disturbances.

648 The rainfall reduction was strong enough to functionally restructure communities in all of its

649 diversity components: communities with higher functional diversity also presented a higher

650 ability to reorganize and adapt to a climatic change scenario, while low functional diversity

651 limits ecosystem resilience.

652 However, despite the distinct impacts of reduced precipitation on functional structure

653 depending on the modeling approach considered, the ability of storing carbon at the

654 ecosystem level did not present significant differences. Our findings highlight the necessity of

655 studies seeking to understand ecosystem resilience to look beyond carbon storage (as is

656 usually done). The functional diversity of a community, and as a consequence, its capacity for

657 reorganization while undergoing change is fundamental for the long-term maintenance of the

658 several ecosystem processes that can be performed by a community (Mori et al., 2013).

659 In addition, like any modeling study, there are simplifications and assumptions that generate

660 caveats that are necessary to be taken into account. The first, and probably the most important,

661 is based on the fact that we have not used variant traits that are connected to drought impacts

662 on plant hydraulics, such as vulnerability to cavitation and embolism. This is especially

663 important considering that several studies have claimed that the decrease in carbon storage

664 due to drought is not, necessarily, linked to a decrease in carbon availability but much more

665 related to hydraulic failure (Eller et al., 2018; Doughty et al., 2015; Phillips et al., 2010;

666 Rowland et al., 2015). Also, our model does not consider the effects of changing functional

> Very valid statement! Also might mirror the fact that unlike our anthropogenic view the "goal" of a given plant individual should be to maximize reproduction rather than C storage?!
> Florian Hofhansl
> 03/04/2021 16:26

667 community to biotic interaction such as competition and facilitation, that seems to play a vital

668 role in determining ecosystem functioning (Mori et al., 2013). In that sense, we strongly

669 recommend that further studies using vegetation models, including CAETÊ, that aim to

670 understand the impacts of drought on carbon stock, should consider plant hydraulics and

671 biotic interactions.

> Both of which we are keen to adress with PlantFATE!
>
> Florian Hofhansl
> 03/04/2021 16:28

672 In summary, the results presented here demonstrate that the proposed trait-based modeling

673 approach enables, as other vegetation models, the exploration of the impacts of climate

674 change in biogeochemical variables but, beyond that, the impacts of these changes on

675 functional diversity and its different components. Thereby, it reinforces the idea that trait-

676 based modeling enables the scientific community to address long-standing research questions

677 posed by functional and community ecology, some of which remained unexplored so far, such

678 as those addressing community assemblage rules and the role of functional diversity for

679 ecosystem functioning.

Acknowledgements

Data availability

685 Model's code, as well as the results, can be found at

686 https://github.com/BiancaRius/CAETE_Rius_etal_2021.

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