

Peer Review Information

Journal: Nature Ecology & Evolution

Manuscript Title: Functional susceptibility of tropical forests to climate change

Corresponding author name(s): Jesús Aguirre-Gutiérrez

Editorial Notes:

Reviewer Comments & Decisions:

Decision Letter, initial version:
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20th October 2021

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Aguirre Gutierrez,

Your manuscript entitled "Functional susceptibility of tropical forests to climate change" has now been seen by 4 reviewers, whose comments are attached. Thank you for your patience while we gathered these reviews.

The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

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* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

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Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[REDACTED]

Reviewer expertise:

Reviewer #1: tropical forests, carbon dynamics, statistics

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Reviewer #2: climate impacts on tropical ecosystems, biogeography

Reviewer #3: forest dynamics, functional ecology

Reviewer #4: tropical forest structure and function

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

I believe this is an important study synthesizing a substantial dataset across a wide range of forests in four continents and a wide range of functional traits. The paper is pleasant to read, clear, concise and well-written, the data and analyses are solid and support the conclusions.

However, I have a few general suggestions and other specific comments which can be helpful to improve the paper.

Major points

My first general comment is that you have not recognized the effects of soil. I understand that obtaining this data is sometimes difficult and that the absence of soil variables does not invalidate your conclusions, however I believe it is important to acknowledge this limitation of the study.

As I understand, when you tested the importance of the continents by leaving each one out of the analyses and checking the correlation of the predictions, you have not accounted for the effect of the number of data points of the continents. Continents with more data points can be more likely to cause stronger shifts in the predictions when dropped from the models. Therefore, I suggest to check if the changes in the correlations are correlated with the number of data points of the dropped continents.

I understand why you expect that the changes (deltas) in climate affect the current patterns. However, one important point should be considered: the changes in climate would be more related to changes in FD/FRed in relation to themselves over time, not necessarily between sites over space. For example, suppose you have two sites, one with FD = 60 and the other with FD = 10 in the past. A change in climate may cause a strong decline in the FD of the first site (suppose a decline of 40), so its FD became 20, and the second site decline 3 units, so its FD became 7. Now suppose that the change in MCWD of the first site was 30 mm and 5 mm for the second site. So, your y vector is [20, 7] and the x vector is [30, 5]. So, there is a positive relationship between changes in MCWD and FD, but if you consider the y vector as the differences [-40, -3] you will see that the relationship is negative and that changes in MCWD actually decreases FD. But if you consider only the current observations [20, 7] you will conclude that increases in drought would increase FD. My point is that it is hard to make inferences about changes in climate on FD if you don't have the changes in FD too. I suggest that you consider this in the discussion as it is an important limitation.



I think the models of the section "Relations between Functional Diversity, Functional Redundancy and Aboveground biomass" can be improved by adding the FD and FRed individual scores together with the bivariate index to evaluate the importance of each one (so you would have: $\Delta \text{AGB} \sim \text{FD} + \text{FRed} + \text{bivariate FD} + \text{plot size}$).

I also believe that it is important to add the changes in climate here to control for its potential effects (although Bennet et al have not found quite important effects of climate), so, now you have: $\Delta \text{AGB} \sim \text{FD} + \text{FRed} + \text{bivariate FD} + \text{changes in MCWD and VPD} + \text{plot size}$. I also believe that it would be good if you perform these analyses with % changes in AGB too and compare its results with the results of the raw changes in AGB. Wouldn't it be expected that FD and FRed were more related to % changes than with raw changes in AGB? For example, in line 298: "...drier tropical forests where ΔAGB was lowest...", if you consider the % this pattern may change.

The point is: the effects of FD-FRed in raw values of ΔAGB can be easily confounded with the fact that forests on favourable climate have both higher biomass (and thus, the changes in AGB would be greater) and FD-FRed, therefore, I believe that add the % changes in AGB will clarify this.

Moreover, as you stated in lines 147-150, the effects of changes in climate would be moderated by FD-FRed. However, it would be necessary to allow FD-FRed to interact with changes in climate, so your model would become: $\Delta \text{AGB} \sim (\text{FD} + \text{FRed} + \text{bivariate FD}) * \text{changes in MCWD and VPD} + \text{plot size}$. With the interactions between changes and climate and FD-FRed you can test if the effect size of changes in climate became weaker as FD-FRed increases. I believe these tests have a better fit to your research questions.

Lines 527-528: Did you tested for spatial autocorrelation (SAC) in the observations or model residuals? The correct way is test for SAC in the models' residuals. So, if you tested for SAC in the observations, I would suggest you to run a linear model with all predictors and then test for SAC in the model's residuals. If you find SAC, you can do the same approach of lines 528-530 with residuals and find the spatial distance to group the plots. Maybe you will not find SAC in models residuals and then you can use a linear model without random effects.

Lines 551-555: The scale of the bivariate index was not clear. How did you obtain the range from 0-30 in the x-axis of Figure 6? It is not clear how the separation in groups (or combination of the FD and FRed values) relates to the scores in the figures 5 and 6.

I also believe that it would be better to use another method to divide the range, such as a k-means with 3 pre-specified groups, it would make the separation more robust and less empirical.

Minor points

Line 83: missing upper case in 1.26 Pg C yr⁻¹

Lines 87-88: "Long-term climate...". This sentence seems isolated here, I believe you can keep this statement here but improving its link with the surrounding text.

Line 94: I think that reference 43 (Allen et al. 2017) is suitable here, together with reference 17.

Lines 109-114: This section is well explained but I missed some recent references. I believe these two

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references below can help you here and in the discussion.

- Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes (Jucker et al. 2014)

- Biodiversity and ecosystem stability: a synthesis of underlying mechanisms (Loreau and de Mazancourt 2013)

Lines 155, line 216: I am not sure if “spatially explicit” is a good choice of words to bring the concept of predictions in space. If you google -spatially explicit models-, you will see that it is related to other concepts and models, which can confuse the readers. I would suggest to write about predictions in space and explain this, instead of using the words “spatially explicit”.

Line 301: typo FD=FRed

Line 329: I think it is safer to drop “stable climatic conditions” from here because the effects of the changes in climate on FD and FRed were positive in most cases. Moreover, the correlations between climate and changes in climate (Fig S6) are small, indicating the wettest sites are not necessarily those with a more stable climate.

Line 526: have you standardized the plot size too?

Lines 528-530: I understood how did you did it, however, I suggest giving more details about this approach.

Line 539-544: Because you added the random effects structure to deal with spatial autocorrelation, the random effects are now part of your study design, therefore it is not necessary to test its inclusion.

It would be good the see the posterior density plots of each coefficient in the supplementary materials (at least).

I also suggest to clarify the priors (you used the rstanarm default priors, right?). You stated in lines 537-538: “effects models were run with normal diffuse priors with mean 0 and 2.5 standard deviation for coefficients and 10 standard deviations for the intercept,..”. These values, 2.5 and 10, were used the adjust the scale/variance based on the data and are not the scale/variance of your prior distributions. So, the scale/variance of the intercept is actually $10 \cdot \text{sd}(y)$ and the scale of the coefficients is actually $(2.5/\text{sd}(x)) \cdot \text{sd}(y)$. I believe you are saying it, but the way you write was ambiguous and some readers may understand that the scale of the priors are 2.5 and 10. I don't think is it necessary to show these formulas, you can just say that 2.5 and 10 were used to adjust the scale and are not the scale themselves. The same is valid for the lines 567-569.

Why did the number of iterations changes from 10000 in line 538 to 5000 in line 569? Convergence problems? It would be good if you say why the number of iterations differed.



Which prior distribution you used for the error? Exponential? Normal?

Section of line 443: I presume that you have not calculated an overall index encompassing the three functional groups together because of the sampling differences between them. It would be good if you explicit this in the methods section.

Section of line 559: How exactly the delta AGB was calculated? The difference between the dates of the last interval before El Niño and the dates of the first interval after El Niño wouldn't matter here? I am sure these details are depicted in the Bennet et al. paper, however, I believe more details about AGB are need here.

Fig 1B: The blue line is difficult to see here, I think the figure will improve if you change the blue color.

Table S2: nutrients functional group is empty

Table S3 – missing text in the header. "The MCWD is the..."

Fig S1: missing upper cases in the units.

Vinícius Maia

Reviewer #2 (Remarks to the Author):

The paper by Aguirre-Gutiérrez et al. analyses how functional diversity (FD) and redundancy (FRed) of tropical forests relate to observed water-related variables and whether higher FD and FRed confer resilience to an extreme event, measured as changes in biomass after an ENSO. The paper is well written, uses an impressive amount of data collected across tropical plot forests and most importantly addresses a key and timing issue, the susceptibility of tropical forests to a changing climate using a trait approach. For sure it will be a great contribution to the readers of Nature Ecology and Evolution. However, I think there are three aspects that need revising to strengthen the outputs/conclusions of this work. First, although the idea of linking FD and FRed with changes in carbon after an extreme event is highly relevant, I believe there are certain circularity issues with the data. Trait data was collected between 2013-2017 (Aguirre-Gutiérrez et al., 2021), and, after proving there is an influence of water-related variables on FD and FRed, data from the projected combined map of these two variables is used to explain changes in biomass after the ENSO, which occurred in 2015. This means that some of the trait values that fed the model may have been affected by the drought caused by ENSO already. If the idea is (as well expressed in the last section of discussion) to use current trait values to assess resilience to future climate only traits measured before the ENSO should be used. From what I see in the data trait data for the African plots was collected in 2015 onwards. Authors may have to rethink what they are showing with this analysis and how it contributes to our understanding of resilience. Second, related to the resilient aspect, I think the authors should clearly state what they mean by "resilience". Across the paper I think they refer to the capacity of keeping most of their ecosystem function(as measured by biomass) before disturbance, however towards the

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end in discussion authors mention results could be useful for biodiversity conservation rather than conservation of ecosystems. This is not a major issue but a clarification (maybe when hypotheses are defined) will help the reader. A third point is the way FD and FRed maps are presented. I find it very useful that the authors have produce a map however it is difficult to assess their uncertainty as 1) calibration points (plots) are not mapped and 2) areas outside calibration range (areas for which MCWD values (and the other variables are outside those used in the model calibration) are not shown. Maybe plots distribution could be added as supplementary information, and fig 3 and fig 4 could differentiate those areas with values outside the calibration range.

Please find other minor comments below:

L. 147-150. Maybe in this hypothesis the concept of resilience can be introduce, as resilience in ecosystem functioning (which is not necessarily resilience in keeping its original floristic composition).

L. 60. is this statement true for all plants or only trees? Please clarify

L. 64 and everywhere else across the text. I think it would be better if the authors use the term "long-term mean MCWD" rather than long-term MCWD as it is more precise.

L. 70. Maybe change "as drought decrease" by "towards drier forests", because you are comparing forests across a water gradient, wetter vs drier.

L. 238-240. This statement about higher FD in wetter areas in the map seems a bit obvious as the map was obtained based on the relationship found in Fig 1 and 2. The next part of the paragraph goes to highlight those areas pointing to the maps. I think a map of MCWD could help the reader to identify those drier/wetter areas. It will help also reading better the results/discussion when talking about specific regions. Maybe the map can be added in sup. map if not enough space on the main text.

L. 285-298. As mentioned in the general comment I think more thought is needed on how the data has been evaluated and the potential circularity problem using traits measured after the dry event. This is specially more concerning because plots used for biomass are all from Africa for which all the trait-climate calibration is based on traits collected 2015-2017. So, from this I would be cautious on saying the traits explain the change in biomass which was measured before the trait measurement. Also, I think the reader will gain much more from this discussion if the ENSO effects on Africa are briefly described (i.e. dry). Having said that it seems that the majority of plots experienced an increase of biomass, and the very few plots that lost biomass are in areas of high FD and FRed. So, I think it could be worth to discuss this more.

L.312. "resilient tropical forest" could the authors please clarify what a resilient tropical forest is? I guess that they refer to those that are able to maintain their main functon(using biomass as a proxy). It might be worth to spell this out as it could also be read as the ones that are able to maintain a floristic composition similar to the one before disturbance.

L. 327-328. I am not sure I follow this, are the authors implying that the Amazon is within the drier range?

L. 328. "The higher diversity in these forests", maybe replace with wet forest? Because in the previous sentence the author refers to both wet and dry forests.

L. 347. Add a comma after "Amazonia".

L. 396. Is it really that your resilience results will contribute to biodiversity conservation if they are focused mostly on biomass? Wouldn't be more ecosystem conservation?

L. 400-402. Not sure you have the evidence to show this based on the points I raised about traits being measured after the extreme event.

L. 406-407. Could the authors please add a map in supplementary material with the location of the plots used for this study?



L. 479-480, Q is mentioned here but not D, although both are mentioned in the previous paragraph, so maybe mention both only once?

L. 494-495. "The MCWD was calculated ref. 13". I think something is missing here?

L. 506. Maybe rephrase as "mean of the full term" (also check the rest of the manuscript).

L. 514. Although defined in the previous section, maybe worth to say "mean MCWD and VPD for the period 1958-2017"

L. 527. Effects on?

L. 561. Either here or in results/discussion mention what the trend of the ENSO was (increase in droughts)

L. 637. Update reference as it is published now.

Other point about discussion

What I am missing here is a discussion about the difference in the spatial patterns of morphological vs nutrient FD as they are quite different. Morphological FD is clearly higher in montane forests across the world while the Nutrient FD has a different pattern, but both FD are related to MCWD, how to explain these different patterns this?

Figures and supplementary material

Figure 1. It was difficult to see the blue line, could the authors please use a lighter grey for the other lines? Also, it took me a while to understand the difference between a and b. Could you explain them in the text separately please?

Figure S1b. It mentions in the caption that the full climatic range is shown across tropical forest, so does that mean that the last value in the x axis is showing the highest value? If that is correct there are areas with values outside the values used to calibrate the model. See my comments above about masking or highlighting these regions in the map as areas with high uncertainty.

Suppl Table S3, caption is incomplete.

Suppl Table S4, figure 3 is mentioned here but it should be figure 5?

References in the suppl mat. Some references have a different caption

Reviewer #3 (Remarks to the Author):

This manuscript deals with very relevant and timely questions, namely the variation in functional diversity and redundancy across tropical forests and its relationships with average and extreme climatic conditions, whose answers to are potentially relevant to management and conservation of those forests. This said, I don't think the approach allows answering them properly, because:

1) None of the traits used is directly linked to plant hydraulic traits and strategies (such as hydraulic resistance, capacitance, root depth, stomata density/size and regulation, deciduousness, NSC, etc), what would be necessary to establish direct relationships with climate and climatic change. And more than individual traits, what plants actually use to deal with the environment are composite designs, sometime called strategies. Having the same value of one trait does not mean having the same strategy, as traits may combine in different designs. Although traits related to carbon acquisition/conservation are expected to correlate with traits related to water acquisition/conservation, this strict match is not necessarily observed (e.g. Baraloto et al 2010), since as mentioned above, trait combinations themselves may change the strategies, and different combinations may lead to the same

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fitness (e.g. Marks & Lechowicz 2006).

2) Although climate is a known driver of trait distributions, other very relevant factors affect them. Among these, soil fertility is a key driver, many times more important than climate (ter Steege et al 2006, Quesada et al. 2012 provide large-scale examples for the Amazon, but the literature is full of demonstrations in all biomes), as it underscores most of the leaf and wood economic spectra. Most of the traits accessed in the study actually tend to vary more in response to fertility than climate. Without a proper control of fertility, it is not possible to know if the responses to climate shown here are correct. Moreover, the interaction of climate and fertility can change in many ways the expected patterns of trait filtering and diversity -- see many examples in Oliveira et al. 2021 -- but here one: Low SLA and low density leaves can be produced by deciduous species in dry places, but also by evergreen species in wet high fertility sites, thus the meaning of the morphological traits is not the same in these contrasting environments. Also, because of the physiological-evolutionary connections between carbon gain and water use, traits that have been selected for one reason (e.g. low fertility driving high wood density) may end up having consequences for other aspects of plant function - e.g. high wood density resisting droughts better (see for example Oliveira et al. 2019).

3) MCWD is used as the sole representation of water availability to plants. However this metric misses completely the contribution of key hydrological sources to the soil water profile, such as groundwater (e.g. Fan 2015) and does not account for soil retention capacity, given by soil properties such as texture. Locally, water availability to plants can vary a lot depending on the topographic heterogeneity, and this variation induces variation in species traits (e.g. Cosme et al. 2017, Oliveira et al 2019). The more topographically heterogeneous the landscape, higher the trait variation can be expected to be. Thus without control of topographic variation, it is not possible to know what is the association of climate to functional variation.

4) The hypothesis that functional diversity is necessarily tied to higher resistance or resilience to climate change, without consideration of the direction of the climatic change, seems naïve. If the environmental change goes in the direction of improving the fit of the average ("optimal") trait values displayed by a community, trait variation is actually bad for the adjustment and will tend to decrease along time. Thus, a real understanding of how climatic change would affect the functional composition requires modelling the direction of change of both climate and trait distribution for each site.

Baraloto, C., Timothy Paine, C. E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., et al. (2010). Decoupled leaf and stem economics in rain forest trees. *Ecol. Lett.* 13, 1338–47. doi:10.1111/j.1461-0248.2010.01517.x.

Cosme, L. H. M., Schiatti, J., Costa, F. R. C., and Oliveira, R. S. (2017). The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol.* 215, 113–125. doi:10.1111/nph.14508

Fan, Y. (2015). Groundwater in the Earth's critical zone: Relevance to large-scale patterns and processes. *Water Resour. Res.* 51, 3052–3069. doi:10.1029/eo064i046p00929-04.

Marks, C. O., and Lechowicz, M. J. (2006). Alternative Designs and the Evolution of Functional



Diversity. *Am. Nat.* 167, 55–66. doi:10.1086/498276.

Oliveira, R. S., Costa, F. R. C., Baalen, E. Van, Jonge, A. de, Bittencourt, P. R., Almanza, Y., et al. (2019). Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytol.* 221, 1457–1465. doi:10.1111/nph.15463.

Oliveira, R. S., Eller, C. B., Barros, F. de V., Hirota, M., Brum, M., and Bittencourt, P. (2021). Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytol.* 230, 904–923. doi:10.1111/nph.17266.

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., et al. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9, 2203–2246. doi:10.5194/bg-9-2203-2012.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., et al. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443, 444–7. doi:10.1038/nature05134.

Detailed comments:

L62. “low functional composition” – there is no such thing. Composition does not have a direction of change, one composition can be different from another, but can’t be higher or lower. In terms of traits or functions, there can be high or low variation or diversity of composition, but still nothing like “low composition”.

L62. “low functional composition and redundancy levels, therefore with diminished capacity to respond to a changing environment.”

This assumption is not necessarily correct. If the environmental change goes in the direction of improving the fit of the average (“optimal”) trait values displayed by a community, trait variation is actually bad for the adjustment and will tend to decrease along time. Thus, a real understanding of how climatic change would affect the functional composition requires modelling the direction of change of both climate and trait distribution for each site.

L71–72 where is the evidence?

If functional variation is tied to climate, it might be difficult or impossible to disentangle what is the cause of forest responses – are the wetter forests more resilient because of the traits or because of the lower climatic variation itself?

L84. MCWD is not an index of soil water availability. It misses completely the contribution of key hydrological sources to the soil water profile, such as groundwater and does not account for soil retention capacity, given by soil properties such as texture. As such, it does not represent plant water availability, unless for very specific conditions. Thus, we should refer to MCWD as an index of climatic water deficit, not anything more.

Locally, water availability to plants can vary a lot depending on the topographic heterogeneity, and this variation induces variation in species traits. The more topographically heterogeneous the

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landscape, higher the trait variation can be expected to be. Thus without control of topographic variation, it is not possible to know what is the association of climate to functional variation.

L88-89. "The MCWD and VPD are effective indicators of drought stress for plants" this is just part of the story, as indicated above.

L145-147. "Tropical wet forests communities, which are more species rich than drier tropical forests, have higher functional diversity given a broader set of ecological strategies available as a result of more stable and favourable climate".

This expectation would be true only if climate alone determined the functional composition and diversity. But we already know this is not the case: several studies show how soil fertility is a key determinant of plant trait filtering, and in the Amazon, for example, this is the dominant filter. The interaction of climate and fertility can change in many ways the expected patterns of trait filtering and diversity -- see many examples in Oliveira et al. 2021 -- but here one: Low SLA and low density leaves can be produced by deciduous species in dry places but also by evergreen species in wet high fertility sites, thus the meaning of the morphological traits is not the same in these contrasting environments.

Also, because of the physiological-evolutionary connections between carbon gain and water use, traits that have been selected for one reason (e.g. low fertility driving high wood density) may end up having consequences for other aspects of plant function (e.g. high wood density resisting droughts better).

Methods

L404. Vegetation plots

We need a histogram of MCWD for these plots, to judge the cover of climatic conditions. However, from the visual scanning of Table S1, I already see there is a strong bias towards drier plots -- only 11 plots (out of 74) with less than 100 mm water deficit MCWD. This sample does not do a good representation of the dominant moist climates in the tropical forest realm. I wonder if the patterns detected reinforce the trends towards the proposed hypotheses given the low representation of moist and wet forests.

L418. "All traits were collected following the GEM network standardised methodology across plots" Give the source for these protocols

L424. "This represented a total sample of 2461 individual trees across the tropics" -- and how many species? Probably there is very little coverage of species diversity

L428-29. Need to state if all the different collection campaigns use the same lab methods for the extraction and measurement of these chemical properties

L439 "when the species had no trait values available, we filled the gaps by averaging the trait values at the genus level"

This is at odds with the affirmation "We collected plant functional trait measurements from the most



abundant species that would cover at least 70% of plot basal area”

L425-432. None of the traits is directly linked to plant hydraulic traits and strategies. The evidence from hydraulics go in the opposite direction to the hypothesis proposed here. Choat et al 2012 show that variation in hydraulic resistance decrease as climate gets wetter. And studies of multiple traits related to hydrological responses, from roots to leaf phenology show a large diversity of hydraulic strategies in dry forests. So I´m not convinced that the effects of functional diversity due to climate and climatic change can be evaluated without consideration of a single hydraulic trait and especially without a combination of them in hydraulic strategies.

Four traits are only different ways of expressing the same thing (LDMC, LWC, DM, FM) and as such inflate the calculation of the functional space without a real contribution to the functional diversity.

L491-495. Was CWD and thus MCWD calculated based on the hydrological year of each plot? Necessary to clarify and account for that, as hydrology is not defined by the calendar year

L497-501. This definition of periods seems odd, and the justification too. The periods should reflect known patterns of variation in climatic trends

L527-533. Good!

Results

L154-163. Instead of an unnecessary repetition of the approach, would be better for the reader if the question is restated before the answer is provided.

I hope the issues raised can be fixed and wish the best for authors.
Flávia Costa

Reviewer #4 (Remarks to the Author):

This manuscript examines links between functional composition and redundancy across a series of pantropical sites in relation to several climate variables. The concepts behind the paper are grounded in ecological theory and the outcome is a new spatial analysis that is compelling. It is a creative use of long-term forest plot data and climate data combined in an innovative way. The results, particularly that drier forests have lower functional diversity and lower functional redundancy, fit what I would have predicted intuitively. The functional diversity and redundancy values are used as proxies for resilience to a changing climate.

While I was impressed by the manuscript, there are a number of things that could be improved. I have listed these below.

1. The biggest improvements need to come with the description of the functional components of the manuscript. I was very confused the first time I read it, and I have finally figured out why.

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a. In many places in the text it is written as if functional diversity and functional redundancy are linked and always go in the same direction, e.g., “high functional diversity and redundancy” (line 71). These two metrics are not always directionally the same and it is crucial that it be written as “high functional diversity and high functional redundancy” (in the case of line 71). There are many more places in the manuscript where this needs to be fixed, e.g., line 149, line 319, line 323, (not a comprehensive list). What the manuscript shows in Figure 5 is correct—that you can have high functional diversity and low functional redundancy or vice versa. For example, I can imagine a dry forest with high functional diversity (many different strategies so niche space is well filled) but because of the climate extremes there is low species richness, meaning that functional redundancy is not high. There were many times where I got confused because the two terms were used together with only one descriptor. And I do believe that more text in the Intro needs to explain the relationship between functional diversity and functional richness. If species richness is held constant, then one would expect more functionally diverse forests to have greater functional redundancy. But if species richness varies (which is the case in these plots), then functional redundancy is in part a function of species richness—in that we expect forests with many species to have more redundancy. I think you could argue that in species-rich forests, we would expect higher redundancy to a greater extent than functional diversity. In a species-poor forest, however, high functional redundancy could be a negative because there may be less adaptability. Therefore, is functional redundancy always a good proxy of climate resilience? See also lines 356–362.

b. The measure of functional diversity is functional dispersion, based on the centroid. So why not call it functional dispersion throughout the manuscript? Functional diversity is a broader term that can encompass several different metrics. Functional dispersion is more exact and fitting for what they have done in this paper.

c. These two functional metrics relate to the traits that are used. The manuscript needs more discussion on the traits chosen. In addition, in Table S1, you can see that most plots have nutrient traits and only a few plots have photosynthetic traits. How does this unevenness in trait data influence the results and interpretation? More acknowledgement of this issue should be included in the Discussion.

d. One key result was that larger changes in moisture lead to more functional dispersion and less functional redundancy—so I could see how this situation would be less resilient and not more resilient (see lines 240–242). That’s a different way of thinking—is that valid?

2. Another missing component is species identity. I feel like this is important in interpreting the manuscript.

a. What are the tree species in these plots, especially in relation to traits? There should be a supplementary table with species and family. Some plots may have lots of congeners and plants in the same family and some may not. Couldn’t these relationships affect the results? For example, Asia has a huge species richness of dipterocarps. So given that, isn’t functional redundancy much higher in the Asian forests? Is this fact an underlying bias?

b. Relate the biogeography to the 70% of the plots basal area—lines 437–442. More thought is needed

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in the Discussion about how the continental differences in families and in number of species/genera might influence the results. Higher species richness likely means higher functional redundancy, but so does the predominance of several families or genera.

3. Some smaller things

a. Figure 6 is confusing. At the top, are the three figures supposed to represent the 3 continents of South America, Africa, and Asia as in the preceding figures?

b. Table S3, what are the site headings? More detail is needed to understand what is in that table.

c. Table S1 has a typo—period and not period.

*****END*****

Author Rebuttal to Initial comments



Response to Reviewers from manuscript (NATECOLEVOL-210914541):

Functional susceptibility of tropical forests to climate change

Aguirre-Gutierrez, Jesus, Berenger Erika, Oliveras, Imma et al.

Reviewer #1 (Remarks to the Author):

R1-1:

I believe this is an important study synthesizing a substantial dataset across a wide range of forests in four continents and a wide range of functional traits. The paper is pleasant to read, clear, concise and well-written, the data and analyses are solid and support the conclusions. However, I have a few general suggestions and other specific comments which can be helpful to improve the paper.

Response:

Thank you for your feedback with constructive and detailed comments which paved the way for an improved manuscript.

R1-2:

My first general comment is that you have not recognized the effects of soil. I understand that obtaining this data is sometimes difficult and that the absence of soil variables does not invalidate your conclusions, however I believe it is important to acknowledge this limitation of the study.

Response:

Our focus for the paper and the models was on the effect of climate rather than on soils, we did this also to keep a focus on what we wanted to analyse and show in the manuscript. However, we recognise the importance of soils which we have shown can have an impact on functional diversity of plants in the tropics (e.g. Aguirre-Gutierrez et al. 2020). Thus following your advice we investigated the possibility of including soil textural and chemistry information in our models. We used the pantropically available soil data from the SoilGrids project (<https://soilgrids.org/>). Although the SoilGrids data is not as exact as plot level soil data this is the best dataset we know of that we could use at a pantropical scale. We selected soil sand and clay content as proxies for water holding capacity of soils and also pH and cation exchange capacity (CEC) for soil fertility. After correlation analysis we selected soil clay content and CEC and included them into our new models. Then we carried out model comparisons by means of leave-one-out cross-validation (LOO) to compare models with and without the soil and found that soil indeed improves the model performance for functional diversity and redundancy models of morphological/structural and nutrient traits but not of photosynthetic traits (see Table S8). We therefore only included the soil data in the morphology/structure and nutrients models but not in the photosynthetic ones also because in the last ones the model tended to overfit given the larger number of covariates and the lower number of data points to fit the model. See new text for methods in lines 595-603 and our new Figures 1 and 2 and Tables S1 and S3.



Aguirre-Gutiérrez, Jesús, et al. "Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity." *Nature communications* 11.1 (2020): 1-10.

R1-3:

As I understand, when you tested the importance of the continents by leaving each one out of the analyses and checking the correlation of the predictions, you have not accounted for the effect of the number of data points of the continents. Continents with more data points can be more likely to cause stronger shifts in the predictions when dropped from the models. Therefore, I suggest to check if the changes in the correlations are correlated with the number of data points of the dropped continents.

Response:

This is a great point to highlight in our manuscript. We carried out the analysis suggested and included a new table, see Table S4, in which we indeed show that in most cases the models depend (and thus the continental predictions for the tropics) on the number of data points used. We have included this information in lines 261-264 of the manuscript.

R1-4:

I understand why you expect that the changes (deltas) in climate affect the current patterns. However, one important point should be considered: the changes in climate would be more related to changes in FD/FRed in relation to themselves over time, not necessarily between sites over space. For example, suppose you have two sites, one with FD = 60 and the other with FD = 10 in the past. A change in climate may cause a strong decline in the FD of the first site (suppose a decline of 40), so its FD became 20, and the second site decline 3 units, so its FD became 7. Now suppose that the change in MCWD of the first site was 30 mm and 5 mm for the second site. So, your y vector is [20, 7] and the x vector is [30, 5]. So, there is a positive relationship between changes in MCWD and FD, but if you consider the y vector as the differences [-40, -3] you will see that the relationship is negative and that changes in MCWD actually decreases FD. But if you consider only the current observations [20, 7] you will conclude that increases in drought would increase FD. My point is that it is hard to make inferences about changes in climate on FD if you don't have the changes in FD too. I suggest that you consider this in the discussion as it is an important limitation.

Response:

We agree with this point and we considered this while designing and writing the first version of our manuscript. One of the main difficulties here is the fact that information on vegetation, traits and functional diversity *per se* across time is seldom available for tropical areas. Thus it is not possible to perform this sort of analysis at a pantropical scale. Still, our expectation was that we would be able to see the possible effects of past climate in present day functional diversity as a type of space-for-time substitution. Following this suggestion we have included this issue in the discussion in lines 427-434:

'An important further step in future analysis will be to include as much information as possible not only on the changes in climate but also on the contemporary changes in



functional diversity and functional redundancy. This would allow establishing a more direct link between the effects of a changing climate and forest functioning. Moreover, while our study showed clear relations with proxies of water availability at a pantropical scale (MCWD and VPD), other environmental variables at fine scale including local topography and ground water availability may also contribute for determining local FD and FRed levels.'

R1-5:

I think the models of the section "Relations between Functional Diversity, Functional Redundancy and Aboveground biomass" can be improved by adding the FD and FRed individual scores together with the bivariate index to evaluate the importance of each one (so you would have: $\Delta \text{AGB} \sim \text{FD} + \text{FRed} + \text{bivariate FD} + \text{plot size}$). I also believe that it is important to add the changes in climate here to control for its potential effects (although Bennet et al have not found quite important effects of climate), so, now you have: $\Delta \text{AGB} \sim \text{FD} + \text{FRed} + \text{bivariate FD} + \text{changes in MCWD and VPD} + \text{plot size}$. I also believe that it would be good if you perform these analyses with % changes in AGB too and compare its results with the results of the raw changes in AGB. Wouldn't it be expected that FD and FRed were more related to % changes than with raw changes in AGB? For example, in line 298: "...drier tropical forests where ΔAGB was lowest...", if you consider the % this pattern may change.

The point is: the effects of FD-FRed in raw values of ΔAGB can be easily confounded with the fact that forests on favourable climate have both higher biomass (and thus, the changes in AGB would be greater) and FD-FRed, therefore, I believe that add the % changes in AGB will clarify this.

R1-6:

Moreover, as you stated in lines 147-150, the effects of changes in climate would be moderated by FD-FRed. However, it would be necessary to allow FD-FRed to interact with changes in climate, so your model would become: $\Delta \text{AGB} \sim (\text{FD} + \text{FRed} + \text{bivariate FD}) * \text{changes in MCWD and VPD} + \text{plot size}$. With the interactions between changes and climate and FD-FRed you can test if the effect size of changes in climate became weaker as FD-FRed increases. I believe these tests have a better fit to your research questions.

Response:

For comments 5 and 6. We have followed your advice by running our models again including the FD and FRed interacting with climate (ΔMCWD and ΔVPD) as suggested, also accounting for size of the plot as before. We did not include the bivariate scores anymore because they were highly correlated to either or both FD and FRed scores:

Pearson's product-moment correlation

FD vs Bivariate Morphology/Structure
Cor= 0.89, t = 18.048, df = 84, p-value < 2.2e-16
FRed vs Bivariate Morphology/Structure
Cor= -0.38, t = -3.7848, df = 84, p-value = 0.0002877
FD vs Bivariate Nutrients
Cor= 0.87, t = 16.516, df = 84, p-value < 2.2e-16
FRed vs Bivariate Nutrients
Cor= -0.67, t = -8.2521, df = 84, p-value = 1.895e-12



FD vs Bivariate Photosynthesis
 Cor= 0.96, t = 32.288, df = 84, p-value < 2.2e-16
 FRed vs Bivariate Photosynthesis
 Cor= 0.11, t = 1.0015, df = 84, p-value = 0.3195

We have included our new results in Table S7 and Figure 6. We have also modified our text in the section entitled 'Testing the link between functional diversity and redundancy and resilience in ecosystem functions under climate change' (lines 334-350) and in our statistical analysis section 'Relations between Functional Diversity, Functional Redundancy and Aboveground biomass' (lines 659-682).

R1-7:

Lines 527-528: Did you tested for spatial autocorrelation (SAC) in the observations or model residuals? The correct way is test for SAC in the models' residuals. So, if you tested for SAC in the observations, I would suggest you to run a linear model with all predictors and then test for SAC in the model's residuals. If you find SAC, you can do the same approach of lines 528-530 with residuals and find the spatial distance to group the plots. Maybe you will not find SAC in models residuals and then you can use a linear model without random effects.

Response:

We indeed tested first for SAC in the raw data and then included the random factor to best define a grouping variable accounting for how the response variable is spatially autocorrelated. We agree that we should check for SAC in the residuals first and then, if needed, include a random factor that minimises the SAC effect. We therefore re-analysed our data with the model construction suggested by the reviewer previously (without a random factor) and only then analysed for SAC in the model residuals using the Moran I test. We now show that the FD models for nutrients and photosynthesis and the FRed model for Nutrients show SAC (see Table S9). We therefore carried out the same analysis described in our original manuscript to include a random factor that groups observations close together to minimise the SAC effect (lines 528-530 in the first version) only for those models mentioned above. We have included our updated methods in the 'Functional Diversity and Functional Redundancy' subsection of the Statistical analysis section in lines 624-644.

R1-8:

Lines 551-555: The scale of the bivariate index was not clear. How did you obtain the range from 0-30 in the x-axis of Figure 6? It is not clear how the separation in groups (or combination of the FD and FRed values) relates to the scores in the figures 5 and 6.

I also believe that it would be better to use another method to divide the range, such as a k-means with 3 pre-specified groups, it would make the separation more robust and less empirical.

Response:

We obtained the 0-30 values from the Bivariate FD-FRed maps where higher values indicated higher FD-FRed scores for a given location. We have 30 values because we have basically 30 colour combinations (5 x 5 matrix). However, given that we followed your suggestions above for the above ground biomass (AGB) models we do



not use the bivariate predictions (scores) any more for the AGB section of analysis. We now rather use the map in Figure 5 to depict the areas with different levels of combined FD and FRed. The grouping of the low, medium and high values was only made for the single FD and FRed maps and not for the bivariate maps; we have clarified this in the main text in lines 645-651.

As we redid our statistical models for this section of analysis, the groupings have also changed; however, the method continues to be the same. We use the frequency distribution and the statistical range of FD or FRed values of each map to then calculate the grouping into low, medium or high FD and FRed value areas. We do not use pre-specified groupings, as such groups would strongly vary among maps (i.e. values for FD photosynthesis may be quite different from the values for FD morphology/structure). Thus, statistically speaking we think it is clearer to show the frequency distribution of values, get the range of values a given map has and divide it into three groups, which will then make the low (groups with smallest values), intermediate (group with intermediate value range) and high (group with larger map values). We have updated our results for this section in lines 283-321.

Minor points

R1-9:

Line 83: missing upper case in 1.26 Pg C yr⁻¹

Response: We have now corrected this.

R1-10:

Lines 87-88: "Long-term climate...". This sentence seems isolated here, I believe you can keep this statement here but improving its link with the surrounding text.

Response: We have updated the text in lines 86-89 as follows: 'Besides impacting the carbon storage capacity of forests, long-term climate and its changes are key drivers of biodiversity declines around the world ^{11, 12,}'

R1-11:

Line 94: I think that reference 43 (Allen et al. 2017) is suitable here, together with reference 17.

Response: We agree and have updated the references accordingly.

R1-12:

Lines 109-114: This section is well explained but I missed some recent references. I believe these two references below can help you here and in the discussion.

- Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes (Jucker et al. 2014)
- Biodiversity and ecosystem stability: a synthesis of underlying mechanisms (Loreau and de Mazancourt 2013)



Response: We have updated the reference in that section as suggested by the reviewer.

R1-13:

Lines 155, line 216: I am not sure if “spatially explicit” is a good choice of words to bring the concept of predictions in space. If you google -spatially explicit models-, you will see that it is related to other concepts and models, which can confuse the readers. I would suggest to write about predictions in space and explain this, instead of using the words “spatially explicit”.

Response:

We have updated the term across the document as suggested and have excluded the term ‘spatially explicit predictions’ to avoid confusing the reader. The changes are as follows:

Line 159: ... in parallel with geographically explicit predictions..

Lines 240-245: Based on our understanding of the relation of FD and FRed of morphological/structural, leaf nutrients and photosynthetic trait groups with climate and soil (Fig. 1 and Fig. 2), and to fill the knowledge gap on the pantropical distribution of functional diversity and redundancy we created pantropical maps of both FD (Fig. 3) and FRed (Fig. 4) distribution. With our map predictions we aim to uncover the locations of forests with possibly higher and lower resilience to a changing climate.

Lines 252-255: We further developed the same statistical models as described above but by removing from the analysis all plots from each continent (Asia and Australia out at the same time) to determine which regions have higher contribution to determining the observed spatial predictions (those of Fig. 5).

Lines 255-258: For morphology/structure, foliar nutrients and photosynthesis we found high correlations between the bivariate maps developed with the full dataset and when Asia/Australia was left out ($r = 0.96, 0.82$ and 0.94 ; Fig. S7, Fig. S8, and Fig. S9 respectively; Also Fig. S10).

Line 294: ..Global predictions....

Line 301: ..Global predictions....

Lines 324: **Global bivariate maps combining ...**

Line 315-316 The bivariate FD-FRed predictions

Lines 645-646: Based on the statistical models described above we created spatial predictions of Functional Diversity (FD) and Functional Redundancy (FRed) at a pantropical scale.

Line 651: We also tested the robustness of the spatial predictions of FD and FRed by also...

Lines 653-654: ...comparing the resulting spatial predictions..

R1-14:

Line 301: typo FD=FRed

Response: The new text is ‘FD-FRed’

R1-15:

Line 329: I think it is safer to drop “stable climatic conditions” from here because the effects of the changes in climate on FD and FRed were positive in most cases. Moreover, the correlations between climate and changes in climate (Fig S6) are small, indicating the wettest sites are not necessarily those with a more stable



climate.

Response: We agree with the suggestion and have deleted the text.

R1-16:

Line 526: have you standardized the plot size too?

Response: Yes, we standardised the plot size term as well and it is now in the text as: 'As some plots were smaller than 1 ha (Table S1) we included the z-scores of plot size as a covariate...'

R1-17:

Lines 528-530: I understood how did you did it, however, I suggest giving more details about this approach.

Response: We have updated the methods also following the reviewer's suggestion from comment R1-7 and we think the methods are now clearer. See lines 606-657.

R1-18:

Line 539-544: Because you added the random effects structure to deal with spatial autocorrelation, the random effects are now part of your study design, therefore it is not necessary to test its inclusion.

Response: Yes, we agree and following the comments from R1-7 and the one above we have updated our methods in line 606-657-650.

R1-19:

It would be good the see the posterior density plots of each coefficient in the supplementary materials (at least).

Response: We have now included posterior density plots for all models and terms in the models and these can now be found in Figures S12 and S13.

R1-20:

I also suggest to clarify the priors (you used the rstanarm default priors, right?). You stated in lines 537-538: "effects models were run with normal diffuse priors with mean 0 and 2.5 standard deviation for coefficients and 10 standard deviations for the intercept...". These values, 2.5 and 10, were used to adjust the scale/variance based on the data and are not the scale/variance of your prior distributions. So, the scale/variance of the intercept is actually $10 \cdot \text{sd}(y)$ and the scale of the coefficients is actually $(2.5/\text{sd}(x)) \cdot \text{sd}(y)$. I believe you are saying it, but the way you write was ambiguous and some readers may understand that the scale of the priors are 2.5 and 10. I don't think it is necessary to show these formulas, you can just say that 2.5 and 10 were used to adjust the scale and are not the scale themselves. The same is valid for the lines 634-637.

Response: We agree and have updated the text in lines 641-650 as suggested.

R1-21:

Why did the number of iterations changes from 10000 in line 538 to 5000 in line



569? Convergence problems? It would be good if you say why the number of iterations differed.

Response: We did this to avoid issues with model convergence and have now specified this in the text in line 637.

R1-22:

Which prior distribution you used for the error? Exponential? Normal?

Response: We used exponential prior for the error term.

R1-23:

Section of line 443: I presume that you have not calculated an overall index encompassing the three functional groups together because of the sampling differences between them. It would be good if you explicit this in the methods section.

Response: Based on the suggestion we have updated the text indicating why it was not suitable to include all traits in an overall index. The new text is as follows: 'We did not build an index including all functional traits together as this would make their interpretation rather difficult as they point to different axes of the global spectrum of plant form and function and also because of the difference in number of records available for each trait group.'

R1-24:

Section of line 559: How exactly the delta AGB was calculated? The difference between the dates of the last interval before El Niño and the dates of the first interval after El Niño wouldn't matter here? I am sure these details are depicted in the Bennet et al. paper, however, I believe more details about AGB are need here.

Response: Following the comment from the reviewer we have included more information in this section as follows in lines 661-674668: 'The plots include censuses from 2000 onward and the median plot size is 1 ha, the mean initial census is May 2008, with the mean pre-El Niño census in April 2014, and mean post-El Niño census in February 2017. The plots have a mean monitoring length pre-El Niño of 8.3 years, with a mean length of the El Niño interval being 2.7 years. To calculate AGB Bennet et al. used the BiomasaFP R package, including the calculation of the census interval corrections for AGB where Pre-El Niño means of these variables are time weighted using the census interval lengths.'

R1-25:

Fig 1B: The blue line is difficult to see here, I think the figure will improve if you change the blue color.

Response: We have changed the dark blue colour to a brighter blue colour that can now be easily seen.

R1-26:

Table S2: nutrients functional group is empty



Response: We have included the term in the first column where it was missing.

R1-26:

Table S3 – missing text in the header. “The MCWD is the...”

Response: We have completed the text of the header.

R1-27:

Fig S1: missing upper cases in the units.

Response: We have improved the legend of Figure S1 as suggested.

Reviewer #2 (Remarks to the Author):

R2-1:

The paper by Aguirre-Gutiérrez et al. analyses how functional diversity (FD) and redundancy (FRed) of tropical forests relate to observed water-related variables and whether higher FD and FRed confer resilience to an extreme event, measured as changes in biomass after an ENSO. The paper is well written, uses an impressive amount of data collected across tropical plot forests and most importantly addresses a key and timing issue, the susceptibility of tropical forests to a changing climate using a trait approach. For sure it will be a great contribution to the readers of Nature Ecology and Evolution.

Response:

Thank you for your constructive comments and advice on how to improve our manuscript, we have taken your suggestions into account and thus have improved our new version of the manuscript.

R2-2:

However, I think there are three aspects that need revising to strengthen the outputs/conclusions of this work.

First, although the idea of linking FD and FRed with changes in carbon after an extreme event is highly relevant, I believe there are certain circularity issues with the data.

Trait data was collected between 2013-2017 (Aguirre-Gutiérrez et al., 2021), and, after proving there is an influence of water-related variables on FD and FRed, data from the projected combined map of these two variables is used to explain changes in biomass after the ENSO, which occurred in 2015.

This means that some of the trait values that fed the model may have been affected by the drought caused by ENSO already. If the idea is (as well expressed in the last section of discussion) to use current trait values to assess resilience to future climate only traits measured before the ENSO should be used. From what I see in the data trait data for the African plots was collected in 2015 onwards.

Authors may have to rethink what they are showing with this analysis and how it contributes to our understanding of resilience.



Response:

The trait data used in the models are not directly affected by ENSO as we do not expect the trait value per se to be able to change from one year to the other (e.g. from before the ENSO in 2014 year to after the ENSO in year 2016). However, we do expect the plant community composition to change right after the extreme event happened and in the years to follow due to mortality, immigration, emigration and competition effects. For an example of the statement above see: Berenguer, Erika, et al. "Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests." *Proceedings of the National Academy of Sciences* 118.30 (2021).

What we are doing in our analysis is to a) go to the field and sample trait values from representative species that can tell us something about the trait composition in the communities; b) assign the trait value at the species level or genus level to each individual in our plots and calculate the community basal area weighted mean value (CWM) of the given trait for that given community; c) then based on those CWM values for the different traits we build our functional diversity (FD) and redundancy indices (FRed); d) we then model the relationship of the indices with climate and make our predictions shown in Figures 3 and 4; e) thus, these maps in Figures 3 and 4 only can tell us something about the overall relationship we expect to find between functional diversity and functional redundancy with climate.

Thus, we agree with the reviewer that such relationships are not really 'time specific' as they are basically averages across a long-time period. Ultimately our FD and FRed maps give insights about what FD and FRed levels would be in a given area based on its long-term water availability conditions (MCWD and VPD as used in our manuscript). Therefore, our analysis of the relationship between above ground biomass (AGB) and FD and FRed (now including interactions with delta climate given comments from Reviewer 1), tell us only how AGB changed and in which locations with which overall levels of FD and FRed. As the reviewer highlights the FD and FRed values predicted in our maps are not tightly linked to the dates of the pre El Niño event but give an overall indication of the diversity and redundancy in trait space of the system.

Following the comment from the reviewer we also investigated the possibility of carrying out an analysis that only uses trait and vegetation data from before the ENSO event. However, this was not viable as much data, not only from Africa but from elsewhere in the tropics, would be left out and we would end up with only few locations to make our models and predictions. Such predictions run the risk of not being representative of the FD and FRed observed in Africa (see for example our analysis in Figures S7 to S9 and Table S4).

We have also modified our text in the section where we explain the link between FD and FRed and AGB as to explicitly state we are working with long-term predictions of FD and FRed. The new text is as follows:

'We tested to what extent the long-term FD and FRed model predictions (Figure 4 and Figure 5), could capture the functioning of tropical forests before and after climatic disturbances such as the 2015 El Niño event. By obtaining the above ground biomass data (AGB) from a set of 86 vegetation plots in tropical Africa before and



after the 2015 El Niño event²⁶ we calculated the relative change in aboveground biomass (% Δ AGB) and modelled it as a function of the predicted long-term FD and FRed maps scores. We show that, on average, larger increases in AGB (Fig. 6; Table S4) can be found at locations that are predicted to have higher FD and FRed of...

We now discuss more in depth the El Niño in Africa and the relationship with the long-term functional diversity and redundancy in lines 435-446:

'...Forests with larger functional diversity and redundancy pools may be more resilient to further climate change. The extreme El Niño events that occur across tropical regions bring about higher temperatures and droughts that can impact the establishment, survival and persistence of tropical forest vegetation, thus also impacting their functioning²⁶. The 2015-2016 El Niño event that affected Africa did not strongly reduce carbon gains in those tropical forests. Although we did not measure the functional composition of those tropical forests in Africa before and after the El Niño event, with our modelling framework we are able to gather a general understanding of the functional diversity and redundancy of such forests given long-term climate conditions. Our results show that in general areas with higher long-term functional diversity and functional redundancy levels tended to be more resilient, i.e. smaller decreases or larger increases in AGB, to changes in environmental conditions such as those caused by the 2015-2016 El Niño event....'

We have also included text in the discussion where we mention the importance of gathering data on functional composition of forest ecosystems across time, which is not really available across tropical forests, see lines 427-434:

'...An important further step in future analysis will be to include as much information as possible not only on the changes in climate but also on the contemporary changes in functional diversity and functional redundancy, this would allow establishing a more direct link between the effects of a changing climate on forest functioning. Moreover, while our study showed clear relations with proxies of water availability at a pantropical scale (MCWD and VPD), other environmental variables at fine scale including local topography and ground water availability may also contribute for determining local FD and FRed levels....'

R2-3:

Second, related to the resilient aspect, I think the authors should clearly state what they mean by "resilience". Across the paper I think they refer to the capacity of keeping most of their ecosystem function (as measured by biomass) before disturbance, however towards the end in discussion authors mention results could be useful for biodiversity conservation rather than conservation of ecosystems. This is not a major issue but a clarification (maybe when hypotheses are defined) will help the reader.

Response:

We have now modified our text in the introduction and at the end of the discussion to make clearer what we mean by resilience and that we are discussing the effects of climate change on the 'ecosystem' *per se*. See below some of the changes made to the text:



Lines 157-158: '...3) There is a positive relationship between functional diversity, functional redundancy and ecosystem functioning (i.e. above ground biomass) as more functionally diverse and redundant communities may decrease the negative effects of a changing climate and may be thought to be thus more resilient.'

Lines 483-485: 'From the ecosystems conservation point of view, it is of critical importance to inform decisions by mapping tropical regions in terms of their resilience to future changes in the environment.'

R2-4:

A third point is the way FD and FRed maps are presented. I find it very useful that the authors have produce a map however it is difficult to assess their uncertainty as 1) calibration points (plots) are not mapped and 2) areas outside calibration range (areas for which MCWD values (and the other variables are outside those used in the model calibration) are not shown. Maybe plots distribution could be added as supplementary information, and fig 3 and fig 4 could differentiate those areas with values outside the calibration range.

Response:

Following the advice from the reviewer we now include maps where we show the calibration points (plots) (Figures S5 and S6), also including maps highlighting areas in climate and soil space that are outside the calibration range (Figure S14) and have updated our text as to highlight this in lines 654-657:

'In Fig. S14 we also highlight locations across the tropics with climate and soil conditions outside of our climatic and soil calibration space, thus not covered by the range in our sampling locations, which may represent locations where our models are extrapolating the relationships found.'

Please find other minor comments below:

R2-5:

L. 147-150. Maybe in this hypothesis the concept of resilience can be introduce, as resilience in ecosystem functioning (which is not necessarily resilience in keeping its original floristic composition).

Response:

Thank you for highlighting this, we have modified the text according to your suggestion, which is now as follows:

'...3) There is a positive relationship between functional diversity and redundancy and ecosystem functioning (i.e. above ground biomass) as more functionally diverse and redundant communities may decrease the negative effects of a changing climate and may be thought to be thus more resilient.'

R2-6:

L. 60. is this statement true for all plants or only trees? Please clarify

Response:

We express this in general terms because we refer to plants in general and not only trees.



R2-7:

L. 64 and everywhere else across the text. I think it would be better if the authors use the term "long-term mean MCWD" rather than long-term MCWD as it is more precise.

Response:

We have modified the text as suggested.

R2-8:

L. 70. Maybe change "as drought decrease" by "towards drier forests", because you are comparing forests across a water gradient, wetter vs drier.

Response:

We found that text in line 170 and have modified it as suggested.

R2-9:

L. 238-240. This statement about higher FD in wetter areas in the map seems a bit obvious as the map was obtained based on the relationship found in Fig 1 and 2. The next part of the paragraph goes to highlight those areas pointing to the maps. I think a map of MCWD could help the reader to identify those drier/wetter areas. It will help also reading better the results/discussion when talking about specific regions. Maybe the map can be added in sup. map if not enough space on the main text.

Response:

We have now included the maps for all covariates used in our models in Figure S3.

R2-10:

L. 285-298. As mentioned in the general comment I think more thought is needed on how the data has been evaluated and the potential circularity problem using traits measured after the dry event. This is specially more concerning because plots used for biomass are all from Africa for which all the trait-climate calibration is based on traits collected 2015-2017. So, from this I would be cautious on saying the traits explain the change in biomass which was measured before the trait measurement. Also, I think the reader will gain much more from this discussion if the ENSO effects on Africa are briefly described (i.e. dry). Having said that it seems that the majority of plots experienced an increase of biomass, and the very few plots that lost biomass are in areas of high FD and FRed. So, I think it could be worth to discuss this more.

Response:

We agree with the reviewer that more discussion about this topic is needed, please also see our reply to this point above in the comment R2-2 and the changes to the text we highlight there. We now discuss more in depth the El Niño in Africa and the relationship with the long-term functional diversity and redundancy in lines 435-446:

'...Forests with larger functional diversity and larger functional redundancy pools may be more resilient to further climate change. The extreme El Niño events that occur across tropical regions bring about higher temperatures and droughts that can impact the establishment, survival and persistence of tropical forest vegetation, thus also impacting their functioning³⁷. The 2015-2016 El Niño event that affected Africa did not strongly reduce carbon gains in those tropical forests. Although we did not



measure the functional composition of those tropical forests in Africa before and after the El Niño event, with our modelling framework we are able to gather a general understanding of the functional diversity and functional redundancy of such forest given long-term climate conditions. Our results show that in general areas with higher long-term functional diversity and functional redundancy levels tended to be more resilient, i.e. smaller decreases or larger increases in AGB, to changes in environmental conditions such as those caused by the 2015-2016 El Niño event....'

R2-11:

L.312. "resilient tropical forest" could the authors please clarify what a resilient tropical forest is? I guess that they refer to those that are able to maintain their main function (using biomass as a proxy). It might be worth to spell this out as it could also be read as the ones that are able to maintain a floristic composition similar to the one before disturbance.

Response:

We have updated the text as suggested in lines 370-373: 'Therefore, determining the distribution of more and less resilient tropical forests (e.g. regarding the maintenance of their functioning) to a changing climate and understanding the mechanisms causing such changes in resilience is pivotal for the conservation of biodiversity and ecosystem functioning.'

R2-12:

L. 327-328. I am not sure I follow this, are the authors implying that the Amazon is within the drier range?

Response:

We mentioned the Amazon as a place where similar analysis had been done and that shows the responses of forests to a changing climate across a water availability gradient. We have rephrased the text to avoid confusion. The new text is found in lines 388-392: 'Such higher functional diversity and higher functional redundancy may be one reason why such forests have experienced weaker compositional changes and in ecosystem functioning (e.g. carbon capture) as a result of a drying climate in comparison to forests in drier areas, as shown for forests across water availability gradients in West Africa ^{31, 32} and the Amazon ^{24, 33}.'

R2-13:

L. 328. "The higher diversity in these forests", maybe replace with wet forest? Because in the previous sentence the author refers to both wet and dry forests.

Response:

We have modified the text as suggested.

R2-14:

L. 347. Add a comma after "Amazonia".

Response:

The text in the paragraph has been updated.

R2-15:



L. 396. Is it really that your resilience results will contribute to biodiversity conservation if they are focused mostly on biomass? Wouldn't be more ecosystem conservation?

Response:

Yes, we agree and have modified the text as suggested.

R2-16:

L. 400-402. Not sure you have the evidence to show this based on the points I raised about traits being measured after the extreme event.

Response:

We did find that wetter tropical forests are in general more functionally diverse and functionally redundant than drier forests and we also found an important relationship between the long-term functional diversity and redundancy and above ground biomass. Although, as described in our response to your previous comments above, we agree that we show just a rough indication of the possible link between the diversity and redundancy indices and the ecosystem functioning and more can be done as to be more accurate when testing this relationship (e.g. measure the functional composition before and after the extreme events).

R2-17:

L. 406-407. Could the authors please add a map in supplementary material with the location of the plots used for this study?

Response:

Yes, the maps are in Figures S5 and S6.

R2-18:

L. 479-480. Q is mentioned here but not D, although both are mentioned in the previous paragraph, so maybe mention both only once?

Response:

We have updated the text as suggested.

R2-19:

L. 494-495. "The MCWD was calculated ref. 13". I think something is missing here?

Response:

We were missing the name of the author and have now rephrased the text.

R2-20:

L. 506. Maybe rephrase as "mean of the full term" (also check the rest of the manuscript).

Response:

We have modified the text as suggested across the manuscript referring to it as 'mean long-term'.



R2-21:

L. 514. Although defined in the previous section, maybe worth to say "mean MCWD and VPD for the period 1958-2017"

Response:

We have modified the text as suggested.

R2-22:

L. 527. Effects on?

Response: We modified the phrase as 'We tested for spatial autocorrelation effects in the FD and FRed model residuals using...'

R2-23:

L. 561. Either here or in results/discussion mention what the trend of the ENSO was (increase in droughts)

Response:

We now provide more information about the ENSO in Africa from the study of Bennett et al. in the discussion in lines 435-446 and also in the methods section in lines 661-668.

R2-24:

L. 637. Update reference as it is published now.

Response:

It seems the reference that was not fully cited was number 33. We have now updated it.

R2-25:

Other point about discussion

What I am missing here is a discussion about the difference in the spatial patterns of morphological vs nutrient FD as they are quite different. Morphological FD is clearly higher in montane forests across the world while the Nutrient FD has a different pattern, but both FD are related to MCWD, how to explain these different patterns this?

Response:

Following your suggestions and those of other reviewers we updated our models also accounting for soil information and thus our maps have also been updated. We have now also updated the text in the results and discussion section to reflect the most up to date information in which we discuss the differences in patterns of distributions between the three trait groups in their functional diversity and functional redundancy.

R2-26:

Figures and supplementary material

Figure 1. It was difficult to see the blue line, could the authors please use a lighter grey for the other lines? Also, it took me a while to understand the difference



between a and b. Could you explain them in the text separately please?

Response:

We changed the old blue colour with a darker one that can be more easily seen. We have also updated figure 1 completely and the text accordingly to reflect the most up to date results. We hope the difference between the subpanels in Figure 1 is now clear.

R2-27:

Figure S1b. It mentions in the caption that the full climatic range is shown across tropical forest, so does that mean that the last value in the x axis is showing the highest value? If that is correct there are areas with values outside the values used to calibrate the model. See my comments above about masking or highlighting these regions in the map as areas with high uncertainty.

Response:

We agree with the reviewer and have taken into account the previous comments to update the manuscript accordingly and included a figure showing those areas out of the data used for model calibration. Please see our responses to the previous related comments.

R2-28:

Suppl Table S3, caption is incomplete.

Response:

We have updated the caption.

R2-29:

Suppl Table S4, figure 3 is mentioned here but is should be figure 5?

Response:

We have modified the text in the Table legend according to the analysis and now it points to the right figures in the main text.

R2-30:

References in the supl mat. Some references have a different caption

Response:

We have updated the references in the supplementary material.

Reviewer #3 (Remarks to the Author):

This manuscript deals with very relevant and timely questions, namely the variation in functional diversity and redundancy across tropical forests and its relationships with average and extreme climatic conditions, whose answers to are potentially relevant to management and conservation of those forests. This said, I don't think the approach allows answering them properly, because:



Response:

We thank the reviewer for taking the time to go through our manuscript and below we give a response to each point raised.

R3-1:

1) None of the traits used is directly linked to plant hydraulic traits and strategies (such as hydraulic resistance, capacitance, root depth, stomata density/size and regulation, deciduousness, NSC, etc), what would be necessary to establish direct relationships with climate and climatic change. And more than individual traits, what plants actually use to deal with the environment are composite designs, sometime called strategies. Having the same value of one trait does not mean having the same strategy, as traits may combine in different designs. Although traits related to carbon acquisition/conservation are expected to correlate with traits related to water acquisition/conservation, this strict match is not necessarily observed (e.g. Baraloto et al 2010), since as mentioned above, trait combinations themselves may change the strategies, and different combinations may lead to the same fitness (e.g. Marks & Lechowicz 2006).

Response:

We fully acknowledge that having information on hydraulic traits is of major importance for quantifying forest response to a changing climate, but in combination with the use of other morphological, structural and photosynthesis-related traits that encompass the water-nutrients-energy acquisition strategies for growth and survival. However, such information on hydraulic traits is seldom available for trait collections across the tropics, which limits its application in pantropical analysis. We now include in our discussion a statement that highlights the need to measure and analyse plant hydraulic traits as captured in the field in order to make a more direct connection between a changing climate and how tropical forest communities may respond to such environmental pressure (lines 467-472):

' Overall, we also highlight the need for measuring more widely other plant functional traits that have a more direct link to the availability, accessibility and transport of water resources such as plant hydraulic traits (e.g. vessel density, P_{50} , hydraulic conductivity, osmotic potential, root size and depth) which are seldom available for most tropical plant species but that may shed more light into the possible responses of tropical forest to a changing climate.'

'None of the traits used is directly linked to plant hydraulic traits' and 'plant strategies'

Recent studies, including that of Shen et al. 2019, have found statistically significant correlations between aboveground and root traits, for instance they found specific leaf area, dry matter, nitrogen and phosphorus content were significant predictors of root tissue density and specific root length, traits that are directly linked to the plant hydraulics system. In our study we in fact make use of those four plant functional traits also measured by Shen et al. 2019. Moreover, Rosas et al. 2019 have demonstrated significant links between leaf mass per area (the inverse of SLA) and the hydraulic trait huber value (sapwood area to leaf area ratio) and also P_{50} (pressure causing 50% xylem embolism), while they also show a significant link between P_{50} and nitrogen levels and nitrogen and huber value. Lastly, Liu et al.



2019 show there is a significant relationship between several leaf morphological/structural traits such as dry matter content, specific leaf area, leaf thickness and hydraulic traits such as stomatal pore length, stomatal density, stomatal pore index and spongy tissue ratio.

Wood density, a trait used in our study, is linked to plant resources acquisition and conservation and also to hydraulic safety and efficiency strategies as shown by Walter et al. 2017.

'Although traits related to carbon acquisition/conservation are expected to correlate with traits related to water acquisition/conservation, this strict match is not necessarily observed (e.g. Baraloto et al 2010).'

We agree with this statement and are familiar with the great literature from Baraloto and colleagues, therefore for our pantropical analysis we gathered the most complete information related to the leaf economics spectrum and to the stem-specific spectrum (here captured with wood density). But see also our response above about the link between hydraulic traits and morphological traits.

The roles of the plant traits we use given a changing climate:

We also define the roles the different morphological/structural, leaf chemistry/nutrients and photosynthetic traits may play under a changing climate (Table S1 in main document). We show there is a plethora of literature (our references in Table S1 are not exhaustive) showing the relation of the functional traits we use and a changing climate.

Specifically, our leaf morphology/structural traits, such as leaf area, specific leaf area, leaf thickness and leaf water content are linked to the plants energy acquisition and leaf transpiration/water loss under a drying climate. Under a drying climate we expect that such traits in the community may change, a mechanism we have already documented for African tropical forests (Aguirre-Gutiérrez et al. 2019 and Aguirre-Gutiérrez et al. 2020, Faucet et al. 2012) but that has also been observed for Amazonian forests (Esquivel-Muelbert et al. 2019; van der Sande et al. 2019). One overarching mechanism encompassing the change in the composition of such traits, as we show for Africa, is the increase in the abundance of deciduous species. Linked to the literature shown above Greenwood et al. 2017 have also shown how tree mortality linked to droughts is tightly related to the plant specific leaf area and wood density traits.

Wood density is relevant for mechanical strengths and is related to stem vulnerability to xylem cavitation. Our expectation is that wood density would be higher in areas with lower water resources, and thus increase with a drying climate. Markesteijn et al. 2011 have also documented how ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits (several used in our study, including wood density) and Chave et al. 2009 highlight the role of wood density for adaptation to different water availability gradients, Poorter et al. 2008 and Poorter et al. 2010 also showed the link between plant maximum height, wood density and rainfall and environmental disturbance.



Nutrients/Chemistry traits: Calcium (Ca) is a regulator in processes related to growth and has direct links to stomatal function and repair of damage from biotic and abiotic stress (Lautner, S., & Fromm 2010). We expect decreases in Ca under increasing droughts and thus an effect on the stomatal functioning which is directly linked to water loss. Potassium (K) plays an important role in the regulation of water status, make a major contribution to the osmotic potential of cells and tissues and it is involved in physiological processes, such as photosynthesis, osmoregulation and stomatal movement (León-Sánchez, Lupe, et al. 2020). Based on recent literature It is expected a decrease in leaf K content with increasing drought. Leaf nitrogen is essential for metabolic reactions involved in light capture, photosynthetic capacity and growth and we have documented changes in this functional trait as a response to increasing droughts in African forests (Aguirre-Gutiérrez et al. 2019).

Photosynthesis traits: Photosynthetic plant rates link to plant strategies within the evergreen to deciduous continuum as adaptations to different water availability conditions. Bucci et al. 2019 show a tight relationship between hydraulic traits and photosynthetic traits such as Amax, a trait we include in our analysis. Moreover, as shown by Grossiord et al. 2020 and Mielke 2005 changes in photosynthesis rates, which are linked to plant growth, are associated to stomatal conductance changes that can be due to increases or decreases in vapour pressure deficit (VPD) levels, thus we expect to capture this interaction in our analysis of functional diversity and redundancy of photosynthetic traits strategies as a function of climatic variables including long-term VPD and its change across the last half century. Moreover, Photosynthetic capacity (Amax, Asat) has also been linked to stem hydraulic conductivity as shown by Santiago et al. 2004 and Brodribb et al. 2000.

Importantly several of the traits outlined above have also been shown to correlate tightly with ecosystem functions (productivity) across successional stages, pointing out the role they play for establishment, growth and survival (see Bongers et al. 2021).

R3-2:

2) Although climate is a known driver of trait distributions, other very relevant factors affect them. Among these, soil fertility is a key driver, many times more important than climate (ter Steege et al 2006, Quesada et al. 2012 provide large-scale examples for the Amazon, but the literature is full of demonstrations in all biomes), as it underscores most of the leaf and wood economic spectra. Most of the traits accessed in the study actually tend to vary more in response to fertility than climate. Without a proper control of fertility, it is not possible to know if the responses to climate shown here are correct. Moreover, the interaction of climate and fertility can change in many ways the expected patterns of trait filtering and diversity -- see many examples in Oliveira et al. 2021 -- but here one: Low SLA and low density leaves can be produced by deciduous species in dry places, but also by evergreen species in wet high fertility sites, thus the meaning of the morphological traits is not the same in these contrasting environments. Also, because of the physiological-evolutionary connections between carbon gain and water use, traits that have been selected for one reason (e.g. low fertility driving high wood density) may end up having consequences for other aspects of plant function - e.g. high wood density resisting



droughts better (see for example Oliveira et al. 2019).

Response:

We thank the reviewer for this great point and we now have improved our models and results by including soil texture and soil chemistry data in our analysis. We selected soil sand and clay content as proxies for water holding capacity and soil pH and cation exchange capacity (CEC) for soil fertility. After correlation analysis we selected soil clay content (%) and CEC (mmol (c)/kg) and included them into our new models. Then we carried out model comparisons by means of leave-one-out cross-validation (LOO) to compare models with and without the soil and found that soil indeed improves the model performance for the functional diversity and redundancy analysis. See new text for methods in lines 591-603 and our new figures 1 and 2 and Tables S1 and S2 but also the new results and discussion section which have been improved accordingly.

R3-3:

3)MCWD is used as the sole representation of water availability to plants. However this metric misses completely the contribution of key hydrological sources to the soil water profile, such as groundwater (e.g. Fan 2015) and does not account for soil retention capacity, given by soil properties such as texture. Locally, water availability to plants can vary a lot depending on the topographic heterogeneity, and this variation induces variation in species traits (e.g. Cosme et al. 2017, Oliveira et al 2019). The more topographically heterogeneous the landscape, higher the trait variation can be expected to be. Thus without control of topographic variation, it is not possible to know what is the association of climate to functional variation.

Response:

We include the maximum climatic water deficit, as the reviewer points out, as a measure of soil water stress and also include in our analysis the vapour pressure deficit which captures effects on plants given the atmospheric water availability. In fact several local key studies on vegetation response to water stress focus on either atmospheric water stress, soil moisture, or deep water access and root traits, or a combination of these, but we rarely have access to all these sources of data, particularly so at a pantropical scale. This does not prevent us from addressing the type of questions we address in our analysis providing that such shortcomings are acknowledged. We also agree on the role that soil texture plays for water retention and thus the possible effect that it may have on local functional diversity and functional redundancy. Thus, as mentioned in our response to your point above we now include soil texture in our analysis (i.e. % clay content). Including soil texture not only improved our models statistically but also improved our understanding of the mechanisms defining plant functional diversity and redundancy across the tropics.

R3-4:

4)The hypothesis that functional diversity is necessarily tied to higher resistance or resilience to climate change, without consideration of the direction of the climatic change, seems naïve. If the environmental change goes in the direction of improving the fit of the average ("optimal") trait values displayed by a community, trait variation is actually bad for the adjustment and will tend to decrease along time. Thus, a real



understanding of how climatic change would affect the functional composition requires modelling the direction of change of both climate and trait distribution for each site.

Response:

Our general hypothesis on the relation between functional diversity and functional redundancy and ecosystem functioning is that the higher diversity and redundancy the more resilient the ecological system may be. This would be the result of a higher capacity/availability of functional strategies to deal with the given environmental pressure, which would then allow continuation of key ecosystem functions (see also Williams et al. 2021; Ashton et al. 2010; Petchey et al. 2004, Bruno et al. 2003). This hypothesis is founded in ecological theory and past research as discussed in the references given above.

We do consider the direction of climate change in our analysis. For both MCWD and VPD we include their change which defines if water availability decreased or increased for a given location and that allows thus to define its role in the functional diversity and redundancy levels of the system.

We respectfully disagree with the statement that 'If the environmental change goes in the direction of improving the fit of the average ("optimal") trait values displayed by a community, trait variation is actually bad for the adjustment'. Following trait driver theory (Enquist et al. 2015), if environmental filtering occurs and if a plant community has the needed functional composition to deal with such new environmental conditions, then it is likely the community composition may change but the forest community as a whole may not disappear or shift towards alternative states (e.g. tropical forest transitioning towards a savanna like vegetation). Thus having a functionally diverse community may actually be beneficial for the persistence of such tropical forests. However, if a given community has a priori a very restricted set of trait values (i.e. low functional diversity) and climate filtering occurs it is highly likely that such community may be strongly impacted by such changes in climate. This would mean that such a system is not resilient to a changing climate and we would expect it to shift towards alternative states.

We do agree with the reviewer that having information on the functional composition before and after climate change occurs is highly valuable. However, such information is seldom available for most sites across the tropics, making it virtually impossible to do the type of analysis we do in our manuscript at a pantropical scale. We now include this in our discussion as a way forward in ecological research (lines 427-434):

'An important further step in future analysis will be to include as much information as possible not only on the changes in climate but also on the contemporary changes in functional diversity and functional redundancy, this would allow establishing a more direct link between the effects of a changing climate on forest functioning. Moreover, while our study showed clear relations with proxies of water availability at a pantropical scale (MCWD and VPD), other environmental variables at fine scale including local topography and ground water availability may also contribute for determining local FD and FRed levels.'



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Grossiord, Charlotte, et al. "Plant responses to rising vapor pressure deficit." *New Phytologist* 226.6 (2020): 1550-1566.

Mielke MS, Almeida AFd, Gomes FP. Photosynthetic traits of five neotropical rainforest tree species: Interactions between light response curves and leaf-to-air vapour pressure deficit. *Brazilian Archives of Biology and Technology*. (2005); 48(5):815-24.

Liu, Congcong, et al. "Variation in leaf morphological, stomatal, and anatomical traits and their relationships in temperate and subtropical forests." *Scientific reports* 9.1 (2019): 1-8.

Enquist, Brian J., et al. "Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories." *Advances in ecological research* 52 (2015): 249-318.

Williams, Laura J., et al. "Remote spectral detection of biodiversity effects on forest biomass." *Nature Ecology & Evolution* 5.1 (2021): 46-54.

Ashton, I. W., Miller, A. E., Bowman, W. D. & Suding, K. N. Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* 91, 3252-3260 (2010).

Petchey, O. L. On the statistical significance of functional diversity effects. *Funct. Ecol.*, 297-303 (2004).

Bruno, J. F., Stachowicz, J. J. & Bertness, M. D. Inclusion of facilitation into ecological theory. *Trends in ecology & evolution* 18, 119-125 (2003).

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543-550.

Brodrribb TJ, Feild TS. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell and Environment* 23: 1381-1388.

Bongers, Franca J., et al. "Functional diversity effects on productivity increase with age in a forest biodiversity experiment." *Nature Ecology & Evolution* (2021): 1-10.



Detailed comments:

L62. “low functional composition” – there is no such thing. Composition does not have a direction of change, one composition can be different from another, but can’t be higher or lower. In terms of traits or functions, there can be high or low variation or diversity of composition, but still nothing like “low composition”.

Response:

We have rephrased our text following your suggestion: ‘...low functional diversity and functional redundancy levels..’

L62. “low functional composition and redundancy levels, therefore with diminished capacity to respond to a changing environment.”

This assumption is not necessarily correct. If the environmental change goes in the direction of improving the fit of the average (“optimal”) trait values displayed by a community, trait variation is actually bad for the adjustment and will tend to decrease along time. Thus, a real understanding of how climatic change would affect the functional composition requires modelling the direction of change of both climate and trait distribution for each site.

Response:

We reply to this comment in the last paragraph of our response to the previous comment.

R3-5:

L71-72 where is the evidence?

If functional variation is tied to climate, it might be difficult or impossible to disentangle what is the cause of forest responses – are the wetter forests more resilient because of the traits or because of the lower climatic variation itself?

Response:

This is presented by the results of our analysis, specifically those shown in Table S7 and Figure 6 for the section ‘Testing the link between functional diversity, functional redundancy and resilience in ecosystem functions under climate change’.

R3-6:

L84. MCWD is not an index of soil water availability. It misses completely the contribution of key hydrological sources to the soil water profile, such as groundwater and does not account for soil retention capacity, given by soil properties such as texture. As such, it does not represent plant water availability, unless for very specific conditions. Thus, we should refer to MCWD as an index of climatic water deficit, not anything more.



Response:

Following the suggestion from the reviewer we have modified our text as follows:
'The Maximum Climatic Water Deficit (MCWD) and Vapour Pressure Deficit (VPD) are effective indicators of drought stress for plants^{13, 14}, with increases in VPD leading to greater plant transpiration stress^{15, 16}.'

R3-7:

Locally, water availability to plants can vary a lot depending on the topographic heterogeneity, and this variation induces variation in species traits. The more topographically heterogeneous the landscape, higher the trait variation can be expected to be. Thus without control of topographic variation, it is not possible to know what is the association of climate to functional variation.

Response:

This text is part of the comment number 3 above for which we gave a response above. Please read our response to this point in point 3. We have also modified the text in the discussion section to express the need to include more information on local topography and possible local water availability for plants. Our new text is as follows:

'An important further step in future analysis will be to include as much information as possible not only on the changes in climate but also on the contemporary changes in functional diversity and functional redundancy, this would allow establishing a more direct link between the effects of a changing climate on forest functioning. Moreover, while our study showed clear relations with proxies of water availability at a pantropical scale (MCWD and VPD), other environmental variables at fine scale including local topography and ground water availability may also contribute for determining local FD and FRed levels.'

R3-8:

L88-89. "The MCWD and VPD are effective indicators of drought stress for plants" this is just part of the story, as indicated above.

Response:

We have modified the word indicators for 'proxies' to be clearer about what we mean in the text about the MCWD and VPD.

R3-9:

L145-147. "Tropical wet forests communities, which are more species rich than drier tropical forests, have higher functional diversity given a broader set of ecological strategies available as a result of more stable and favourable climate".

This expectation would be true only if climate alone determined the functional composition and diversity. But we already know this is not the case: several studies



show how soil fertility is a key determinant of plant trait filtering, and in the Amazon, for example, this is the dominant filter. The interaction of climate and fertility can change in many ways the expected patterns of trait filtering and diversity -- see many examples in Oliveira et al. 2021 -- but here one: Low SLA and low density leaves can be produced by deciduous species in dry places but also by evergreen species in wet high fertility sites, thus the meaning of the morphological traits is not the same in these contrasting environments. Also, because of the physiological-evolutionary connections between carbon gain and water use, traits that have been selected for one reason (e.g. low fertility driving high wood density) may end up having consequences for other aspects of plant function (e.g. high wood density resisting droughts better).

Response:

We have included the role of suitable soil conditions in our hypothesis, which reflects the use of soil texture and chemistry in our new analysis, see also the methods section on the use of soil CEC and Clay. The comment is the same as in comment number 2, please see a full response above (response 2).

R3-10:

Methods

L404. Vegetation plots

We need a histogram of MCWD for these plots, to judge the cover of climatic conditions. However, from the visual scanning of Table S1, I already see there is a strong bias towards drier plots -- only 11 plots (out of 74) with less than 100 mm water deficit MCWD. This sample does not do a good representation of the dominant moist climates in the tropical forest realm. I wonder if the patterns detected reinforce the trends towards the proposed hypotheses given the low representation of moist and wet forests.

Response:

In Figure S2 we show how our sampling locations cover a wide range of the climatic conditions available across the tropics where tropical and subtropical dry and moist broadleaf forests exist. For instance many of our plots are located in wet tropical forests in Southern Mexico, Panama, Brazil, Peru, Malaysia, Gabon and Australia and also in these regions we have plots that are located in drier locations. In our new manuscript we show the maps of all covariates used in our models in Figure S3 and in Figure S4 and depict how our sampling locations are widely distributed in climate and soil space using principal component analysis. Lastly in Figure S5 and S6 we show the distribution of our sampling locations across the tropics. Overall, our plots are distributed all across the climate space available in the study area (Figure S2).

R3-11:

L418. "All traits were collected following the GEM network standardised methodology



across plots” Give the source for these protocols

Response:

We give the references in the main text when we introduce each of the traits in the plant functional traits section of the methods. The references are:

Martin, R. E. *et al.* Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Frontiers in plant science* **10**, 1810 (2020).

Enquist, B. J. *et al.* Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Global Ecol. Biogeogr.* **26**, 1357-1373 (2017).

Both, S. *et al.* Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytol.* **221**, 1853-1865 (2019).

Oliveras, I. *et al.* The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Frontiers in Forests and Global Change* **3**, 18 (2020).

Gvozdevaite, A. *et al.* Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–savanna boundaries in Ghana and Brazil. *Tree Physiol.* **38**, 1912-1925 (2018).

Aguirre-Gutiérrez, J. *et al.* Pantropical modelling of canopy functional traits using Sentinel-2 remote sensing data. *Remote Sens. Environ.* **252**, 112122 (2021).

R3-12:

L424. “This represented a total sample of 2461 individual trees across the tropics” – and how many species? Probably there is very little coverage of species diversity

Response:

We had 1611 species with traits collected in our plot data.

R3-13:

L428-29. Need to state if all the different collection campaigns use the same lab methods for the extraction and measurement of these chemical properties

Response:

For each of the traits and field campaigns we provide detailed references which describe the protocol used:

Malhi, Yadvinder, et al. "The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics." *Biological Conservation* 253 (2021): 108889.



Martin, R. E. *et al.* Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Frontiers in plant science* **10**, 1810 (2020).

Enquist, B. J. *et al.* Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Global Ecol. Biogeogr.* **26**, 1357-1373 (2017).

Both, S. *et al.* Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytol.* **221**, 1853-1865 (2019).

Oliveras, I. *et al.* The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Frontiers in Forests and Global Change* **3**, 18 (2020).

Gvozdevaite, A. *et al.* Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest-savanna boundaries in Ghana and Brazil. *Tree Physiol.* **38**, 1912-1925 (2018).

Aguirre-Gutiérrez, J. *et al.* Pantropical modelling of canopy functional traits using Sentinel-2 remote sensing data. *Remote Sens. Environ.* **252**, 112122 (2021).

R3-14:

L439 "when the species had no trait values available, we filled the gaps by averaging the trait values at the genus level"

This is at odds with the affirmation "We collected plant functional trait measurements from the most abundant species that would cover at least 70% of plot basal area"

Response:

Yes, we specify that at least 70% of the basal area is covered with trait data. In some locations if the species had been already collected in a neighbouring plot it was not collected again in a different plot. This is the reason for the trait value assignment.

R3-15:

L425-432. None of the traits is directly linked to plant hydraulic traits and strategies. The evidence from hydraulics go in the opposite direction to the hypothesis proposed here. Choat et al 2012 show that variation in hydraulic resistance decrease as climate gets wetter. And studies of multiple traits related to hydrological responses, from roots to leaf phenology show a large diversity of hydraulic strategies in dry forests. So I'm not convinced that the effects of functional diversity due to climate and climatic change can be evaluated without consideration of a single hydraulic trait and especially without a combination of them in hydraulic strategies.

Response:

We agree that having hydraulic trait data is of major importance to advance this research field, however, as the reviewer may be aware, there is no such information available at wide spatial scale. Therefore to advance the field of study with the data



that it is readily available we selected plant functional traits that have been shown to have a link with the response of plants to climate. We give a full list of the traits, their possible role and reference to why they may be important for the plants responses to climate change (see reply to the first comment above). Lastly, we did use one trait highly related to plant hydraulics, i.e. wood density (reference to this in our response to the first comment above). Moreover, in our response to the first comment we also give references to the close relationship there is between several of the traits used in our study and hydraulic traits. In our main text we now also acknowledge the importance of collecting plant hydraulic traits in order to advance the field of trait-based ecology under a changing climate (please see the new text also in our response to your first comment).

R3-16:

Four traits are only different ways of expressing the same thing (LDMC, LWC, DM, FM) and as such inflate the calculation of the functional space without a real contribution to the functional diversity.

Response:

Those traits represent slightly different characteristics of the leaf as water content does not correlate exactly to dry mass or fresh mass. However, we see the point of the reviewer that they are highly related to each other. However, our diversity indices do not get inflated given that in the worst case scenario they would not render any new information into the diversity axes and thus would not count to increase the diversity values (see also Laliberté et al. 2010).

Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299-305 (2010).

R3-17:

L491-495. Was CWD and thus MCWD calculated based on the hydrological year of each plot? Necessary to clarify and account for that, as hydrology is not defined by the calendar year

Response:

We used the most negative value of the year using a running window of 12 months starting in the first month with climatic data which in our case was January, we have specified this now in the methods. So yes, these metrics are based on the hydrological year.

R3-18:

L497-501. This definition of periods seems odd, and the justification too. The periods should reflect known patterns of variation in climatic trends

Response:



We follow the recommendations from the World Meteorological Organization in order to characterise the average weather conditions for a given area and they recommend using a climatology of at least 30 years (www.wmo.int/pages/prog/wcp/ccl/faqs.php). Therefore, as we wanted to calculate the change in climatic conditions restricted also to the availability of data we ended up using the years 1958-1987 (30 years climatology) representing the average conditions of the first time period and the 1988-2017 to represent the climatology of the second time period (so average present day conditions).

R3-19:

L527-533. Good!

Response:

Thank you.

R3-20:

Results

L154-163. Instead of an unnecessary repetition of the approach, would be better for the reader if the question is restated before the answer is provided.

Response:

Here we wanted to remind the reader about what we are doing and how we are doing it as in the introduction there is not enough space to do this. Given your comments and those of the other three reviewers we have modified a large part of our analysis and therefore the text of our manuscript. Thus we hope that the new analysis and way of writing the results in the main text are clearer and more concise than before. Please see the new version of the manuscript in which we hope we have successfully addressed this comment and the ones above.

Reviewer #4 (Remarks to the Author):

R4-1:

This manuscript examines links between functional composition and redundancy across a series of pantropical sites in relation to several climate variables. The concepts behind the paper are grounded in ecological theory and the outcome is a new spatial analysis that is compelling. It is a creative use of long-term forest plot data and climate data combined in an innovative way. The results, particularly that drier forests have lower functional diversity and lower functional redundancy, fit what I would have predicted intuitively. The functional diversity and redundancy values are used as proxies for resilience to a changing climate.

R4-2:

While I was impressed by the manuscript, there are a number of things that could be improved. I have listed these below.



Response:

Thank you for your comments and advice, which has allowed us to improve our manuscript. Below we respond to each comment and explain how we have taken into account each point you raise as to improve the manuscript.

R4-3:

1. The biggest improvements need to come with the description of the functional components of the manuscript. I was very confused the first time I read it, and I have finally figured out why.

a. In many places in the text it is written as if functional diversity and functional redundancy are linked and always go in the same direction, e.g., “high functional diversity and redundancy” (line 71). These two metrics do not always directionally the same and it is crucial that it be written as “high functional diversity and high functional redundancy” (in the case of line 71). There are many more places in the manuscript where this needs to be fixed, e.g., line 149 line 319, line 323, (not a comprehensive list). What the manuscript shows in Figure 5 is correct—that you can have high functional diversity and low functional redundancy or vice versa. For example, I can imagine a dry forest with high functional diversity (many different strategies so niche space is well filled) but because of the climate extremes there is low species richness, meaning that functional redundancy is not high. There were many times where I got confused because the two terms were used together with only one descriptor.

Response:

We appreciate the comment from the reviewer and have modified the text as suggested now writing in full when we refer to functional diversity and/or functional redundancy and to their descriptors.

R4-4:

And I do believe that more text in the Intro needs to explain the relationship between functional diversity and functional richness. If species richness is held constant, then one would expect more functionally diverse forests to have greater functional redundancy. But if species richness varies (which is the case in these plots), then functional redundancy is in part a function of species richness—in that we expect forest with many species to have more redundancy. I think you could argue that in species-rich forests, we would expect higher redundancy to a greater extent than functional diversity. In a species poor forest, however, high functional redundancy could be a negative because there may be less adaptability. Therefore, is functional redundancy always a good proxy of climate resilience? See also lines 356–362.

Response:

We argue that one metric separately from the other (i.e. only functional diversity or only functional redundancy) cannot render enough information about the possible resilience of tropical forests to a changing climate. This is why we present Figure 5 in the main text where we combine both estimates, functional diversity and functional redundancy, as to uncover regions where both may be lowest (gray colours in Figure 5) and where both are maximised (purple colours in Figure 5). As also shown in other studies with different taxa (e.g. Arruda et al. 2018; Aguirre-Gutierrez et al. 2017) species richness and functional diversity may not always be highly correlated. Moreover, arguably different functional traits may respond differently to different



drivers of change (e.g. temperature or precipitation change) showing differences in the diversity indices but not necessarily in the species richness (Cadotte et al. 2011). We have updated our introduction following your advice and including as much detail as possible on the species richness-diversity relation and giving the references stated above. However, we could not expand so much on this topic as we wanted in the introduction as we are limited by the word count of the journal and we are already over the word count allowed.

Our new text in the introduction is as follows (see lines 105-124): 'Ecosystem resilience may increase through different pathways, for example, by species having the same traits that affect a given ecosystem process, such as carbon capture, but different traits to respond to environmental changes, such as droughts. Arguably different functional traits may respond differently to different drivers of change (e.g. temperature or precipitation change) which may be reflected in trait diversity but not necessarily in species richness²¹ given that there is not always a tight relation between species richness and functional trait diversity^{22, 23}. According to the biodiversity-ecosystem functioning insurance hypothesis²⁴, ecosystem functions should be less affected by a changing environment when 1) the ecosystem possesses both high functional diversity (e.g. large range of trait values; FD), 2) but also a wide set of species with similar functional characteristics²⁴ conferring the system with high functional redundancy (FRed)^{25, 26}. Thus, in communities with high functional diversity and high functional redundancy, the loss of a given species is less likely to result in the disruption of the ecosystem function²⁷, as other species will probably continue carrying out the same functions, substituting the lost species^{28, 29}. High FD and high FRed may enhance the temporal stability of ecosystem functions (e.g., biomass productivity)³⁰ and thus provide a buffering effect against environmental changes²⁴, conferring higher resilience. Nonetheless, these hypotheses have never been tested across the tropics, and the role of FD and FRed for maintaining the tropical forests ability to capture and store carbon remains to be tested and quantified at this global scale. Quantifying the FD and FRed is crucial to advancing our understanding of the resilience of these forests in the Anthropocene.'

Arruda Almeida, Bia de, et al. "Comparing species richness, functional diversity and functional composition of waterbird communities along environmental gradients in the neotropics." *PloS one* 13.7 (2018): e0200959.

Aguirre-Gutiérrez, Jesús, et al. "Butterflies show different functional and species diversity in relationship to vegetation structure and land use." *Global Ecology and Biogeography* 26.10 (2017): 1126-1137.

Cadotte, Marc W., Kelly Carscadden, and Nicholas Mirotchnick. "Beyond species: functional diversity and the maintenance of ecological processes and services." *Journal of applied ecology* 48.5 (2011): 1079-1087.

R4-5:

b. The measure of functional diversity is functional dispersion, based on the centroid. So why not call it functional dispersion throughout the manuscript? Functional



diversity is a broader term that can encompass several different metrics. Functional dispersion is more exact and fitting for what they have done in this paper.

Response:

We agree there are several metrics related to functional diversity and this is why we first defined which is the one we use. Once the functional diversity metric is defined, in our case functional dispersion, we think it is important to use a term that can be generalised and easily understood and applied by the broad readership of the journal. A simple and general term like functional diversity may be better understood than a much more specific one as functional dispersion. We however believe it is important the term is clearly defined and thus we have included its definition in the introduction section (line 146) besides its description in the methods section.

R4-6:

c. These two functional metrics relate to the traits that are used. The manuscript needs more discussion on the traits chosen. In addition, in Table S1, you can see that most plots have nutrient traits and only a few plots have photosynthetic traits. How does this unevenness in trait data influence the results and interpretation? More acknowledgement of this issue should be included in the Discussion.

Response:

Following the advice from the reviewer we have updated our introduction to describe the traits used and why they are important under a changing climate, we still reference Table S1 as the main source of full information about the traits and their importance.

Our new text is as follows (lines 125-137): 'Here, we address this knowledge gap by combining a new pantropical dataset of 16 plant traits related to morphology/structure (leaf area, leaf dry and fresh mass, leaf dry matter content, leaf water content, specific leaf area, leaf thickness, wood density), foliar nutrients (leaf calcium, potassium, magnesium, nitrogen and phosphorus content) and photosynthesis (photosynthetic rate, dark respiration). These plant traits are hypothesised to be of importance for tropical forests to adapt or respond to a drying climate (see Table S1 for a description on their hypothesised importance). The importance of such traits relies on their influence on the capacity of species to capture energy for growth and conserve resources (e.g. water) for survival under stressful environmental conditions, such as droughts, and have been shown to change in response to a changing climate^{31, 32, 33}. The plant traits were collected from 2461 individual trees belonging to 1611 species distributed across 74 plots that contained 32,464 individual trees equal to or greater than 10 cm diameter at breast height from 2497 species (Fig. S1, Table S2, See Methods).'

We tested for the correlation between the number of records used to fit the models and the FD-FRed bivariate maps (Figure 5) and when leaving one continent out of model fitting at a time (Figures S7-S9). We show that the number of records influenced the final predictions (Table S4) and state this in the main text in lines 258-264:

'For morphology/structure and photosynthesis there were also high correlations when Africa was left out of model fitting ($r = 0.92$ and 0.93 respectively; Fig. S7 and Fig. S9 respectively). Such unique contributions to the models from the different regions depict those regions contributed significantly for the full model predictions



(Fig. S10), which is also correlated to the number of observations available for each continent (Table S2 and Table S4).'

R4-7:

d. One key result was that larger changes in moisture lead to more functional dispersion and less functional redundancy—so I could see how this situation would be less resilient and not more resilient (see lines 240-242). That's a different way of thinking—is that valid?

Response:

Overall, we show that areas that have higher average long-term soil (MCWD) and atmospheric (VPD) water deficits (i.e. drier forests) tend to be less functionally diverse and also less functionally redundant than wetter areas. When we detected an important effect of changes in MCWD on functional diversity and/or functional redundancy this was often mediated by the VPD but in general functional diversity and functional redundancy was lower in areas that increased their MCWD and VPD (see our new Figures 1 and 2 that now include the role of soil chemistry and texture). The effects of changes in moisture, as the reviewer mentions, would depend on where they happen, i.e. in dry or wet tropical forests, and whether they impact the functioning of the forest (e.g. modifying the above ground biomass). If the functional diversity and functional redundancy levels change given a changing climate but the functioning of the ecosystem continues being equal (e.g. above ground biomass) than before or increases then in the context of our manuscript we could state the forests are resilient to those changes in climate that occurred.

R4-8:

2. Another missing component is species identity. I feel like this is important in interpreting the manuscript.

a. What are the tree species in these plots, especially in relation to traits? There should be a supplementary table with species and family. Some plots may have lots of congeners and plants in the same family and some may not. Couldn't these relationships affect the results? For example, Asia has a huge species richness of dipterocarps. So given that, isn't functional redundancy much higher in the Asian forests? Is this fact an underlying bias?

Response:

We acknowledge that showing a list with the species available in each plot and the link to their traits is a great piece of information, however, we cannot make it freely available at this stage given the conditions imposed to us by the data owners who are also working with their data and would like to publish their work before making it freely available. However, we can summarise the species found per country or in general the ones used in our study without separating per country. This table would have at least 2849 rows and thus it is not viable to include it as supplementary information. We propose that once the paper is accepted we can make such a list available through a permanent open access repository. Having many congeners in the same plot or region may have an effect on the resulting indices in case the traits under study show phylogenetic conservatism. However, based on our previous analysis (e.g. Aguirre-Gutierrez et al. 2019 and Aguirre-Gutierrez et al. 2020) we have seen most traits here used lack a phylogenetic signal. Moreover, in our analysis we used diversity and redundancy metrics that have been shown to be



unaffected by species richness (van der Plas et al. 2017). Thus, to us it makes sense to have high redundancy in areas such as Malaysian Borneo if the traits would have a phylogenetic signal and if this was the case that would not be considered a bias but a valid ecological reality of such study area, which may actually confer such forests resilience to changes in climate. Moreover, in our analysis and results (Figure 4) we do see that forests in Malaysia have intermediate to high redundancy scores but are not, however, the only ones with such scores and are also not predicted to be the ones with the highest functional redundancy scores across the tropics.

Aguirre-Gutiérrez, Jesús, et al. "Drier tropical forests are susceptible to functional changes in response to a long-term drought." *Ecology letters* 22.5 (2019): 855-865.

Aguirre-Gutiérrez, Jesús, et al. "Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity." *Nature communications* 11.1 (2020): 1-10.

van der Plas, F., Van Klink, R., Manning, P., Olff, H. & Fischer, M. Sensitivity of functional diversity metrics to sampling intensity. *Methods in Ecology and Evolution* 8, 1072-1080 (2017).

R4-9:

b. Relate the biogeography to the 70% of the plots basal area—lines 437-442. More thought is needed in the Discussion about how the continental differences in families and in number of species/genera might influence the results. Higher species richness likely means higher functional redundancy, but so does the predominance of several families or genera.

Response:

This is a great point that we now include in the results (lines 265-273) and discussion in lines 381-385:

'In our study we observed that the functional diversity levels are not significantly related to the taxonomic diversity found in the study sites across the tropics but that functional redundancy tends to be, especially for redundancy in morphological/structure and foliar nutrients traits. This points to the role of taxonomic diversity on the possible resilience of tropical ecosystems.'

We have carefully considered after carrying out analysis looking into the relationship between taxonomy and the FD and FRed metrics. When thinking about the points made and questions raised by the reviewer we carried out an analysis looking into the correlation between the FD and FRed of morphological/structural, nutrients and photosynthesis trait groups and the number of species, genera and families found in the plots. While, we do not find any significant Pearson correlation coefficient ($P_{val} > 0.05$) for most of the FD comparisons, actually only between FD photosynthesis and number of families in the plot, we did find significant correlations, although low in most cases (i.e. < 0.6 ; $P_{val} < 0.05$) between FRed of morphology/structure, FRed nutrients and the number of species, genus and family. Thus in the discussion we now include text that explains that at least some of the patterns observed for the functional redundancy of those trait groups could be linked



to their taxonomy richness, specifically when looking into the functional redundancy of the morphological/structural and nutrients traits. The new text is as follows:

Lines 265-271:

'As predicted, our results show that wetter tropical forests tend to be more functionally diverse than drier tropical forests, especially for morphological/ structural traits and foliar nutrients traits, but also more functionally redundant for foliar nutrients and photosynthetic traits than drier tropical forests (Fig. 3 and Fig. 4). While FD levels across our sampling locations are not significantly related to their taxonomic diversity (number of species, genera and families; $P\text{-val} > 0.05$), $FRed_{NU}$ appears to be positively correlated to taxonomic diversity ($P\text{-val} < 0.05$; Table S5).'

Lines 374-385:

'Theory on niche complementarity predicts that more diverse systems make more efficient use of ecosystem properties given the complementarity of species in the use of resources available^{39,40}. Such complementarity may also increase the performance of diverse communities in the face of more stressful environments given facilitative interaction between species⁴¹. It can be therefore expected that more functionally diverse and more functionally redundant communities would experience lower change in performance (e.g. lower mortality, lower biomass decrease) with changes in environmental conditions (e.g. $\Delta MCWD$, ΔVPD). In our study we observed that the functional diversity levels are not significantly related to the taxonomic diversity found in the study sites across the tropics but that functional redundancy tends to be, especially for redundancy in morphological/structure and foliar nutrients traits. This points to the role of taxonomic diversity on the possible resilience of tropical ecosystems.'

R4-10:

3. Some smaller things

a. Figure 6 is confusing. At the top, are the three figures supposed to represent the 3 continents of South America, Africa, and Asia as in the preceding figures?

Response:

We have modified Figure 6 and also improved its legend. We hope it is now clearer for interpretation.

R4-11:

b. Table S3, what are the site headings? More detail is needed to understand what is in that table.

Response:

Table S3 shows the statistical model results investigating the relation between FD, $FRed$ and the climatic and soil conditions across the tropics. We have modified our table including the legend and the variables descriptions and hope it is now easier to interpret the results.

R4-11:

c. Table S1 has a typo—period and not period.

Response:



We corrected the typo (extra 'o') in the word 'periodo'.



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Decision Letter, first revision:

8th February 2022

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Aguirre Gutierrez,

Your manuscript entitled "Functional susceptibility of tropical forests to climate change" has now been seen by our original four reviewers, whose comments are attached. Some of the reviewers have some remaining concerns that will need to be addressed before we can offer publication in *Nature Ecology & Evolution*. We will therefore need to see your responses to these queries, along with a revised manuscript, before we can reach a final decision regarding publication. We certainly hope that we will be able to offer publication of the paper following the next revision, but feel we need to send the revised paper to Reviewers 1 and 3 (only) before we make that decision.

I hope that responding to Reviewer 1's remaining points will be quite straightforward.

With regard to Reviewer 3's review: we understand that the more conceptual point about the relationship between diversity and ecosystem resilience, and the use of this relationship in producing "maps of resilience", is to a certain degree a matter of opinion. We would not expect maps to be removed from your paper, but suggest that some discussion of the need for caution around inferences made from this relationship, particularly when used to guide conservation and management efforts, be added to your paper. We will need to obtain Reviewer 3's input on your responses to their remaining more technical concerns regarding traits indirectly linked to drought responses, and regarding other determinants of water stress to plants - as well as their minor points.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to

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any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

[REDACTED]

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit <http://www.springernature.com/orcid>.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[REDACTED]

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

To the authors,

I believe the authors did a good job reviewing the manuscript and the manuscript has improved a lot. In this second round of review, I raised some points that were not clear or could be improved before publication.

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In your response to R2-2, if I understand correctly, you mentioned that delta AGB was actually relative delta AGB %, but in the manuscript it's still delta AGB. Have you used raw or relative delta AGB?

The slopes in the Figure 6 are the interaction slopes instead of the slopes, it may confuse some readers. I suggest to make clear that the slope values in the figures are not the slope of the variables of the X axis, but the slope of the interactions between the variables in the X axis and the moderator.

Regarding the response for R1-4, I appreciated that the authors recognized this limitation in the discussion. However, I would suggest to add a statement in the introduction and/or methods recognizing that these relationships are proxies of the effects of climate change on FD and that this limitation exists. More specifically, I believe that this limitation is very important and should be mentioned at least in the materials and methods when the context is introduced.

In the responses for R1-5 and R1-6 the authors have not mentioned what they think about using the relative values of delta AGB. I am even more confused because of their response to R2-2 where they mentioned the % delta AGB. Could the authors show the correlation between % and raw changes in AGB?

Vinícius Maia

Reviewer #2 (Remarks to the Author):

The authors have extensively responded to the comments made by the reviewers and have incorporated most of the suggestions that were made. Therefore, they have absolved any concerns I had. I think this would be a great paper for the readers of Nature Ecology and Evolution. I only have 3 minor comments:

l. 118, maybe replace substituting by compensating? Substitutes seem that the species was not having that role before?

l.435-437 Enso causes anomalous high precipitation in tropical coastal areas so better specify droughts are observed in tropical rainforest.

l. 478-479 Is something is wrong with this sentence (grammar)?

Reviewer #3 (Remarks to the Author):

Dear authors,

I see that you have worked on some of the major technical issues, e.g. the inclusion of soil layers, which indeed proved relevant as me and another reviewer have indicated. However, I also see that you have taken some conceptual and technical points too lightly, which in my perspective weaken this

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contribution.

The conceptual point is the theoretical basis for the use of FD and Fred in the prediction of ecosystem susceptibility to change. Although the published literature posit the hypothesis that higher functional diversity should lead to higher ecosystem resistance/resilience, through the insurance effect, this hypothesis lacks important parameters: where the system starts (in terms of the traits mean and amplitude), the intensity and direction of the environmental change, and the time scale. A functionally diverse community with trait means and amplitude very far from that required to cope to the intensity of the change can be expected to have a much poorer response (and eventually totally collapse) than a community whose traits are less diverse but close to those required to deal with the new conditions. A community in between (with some functional diversity, but still not too close to the direction of change) can be expected to have some elements surviving (those with adequate traits for the new conditions) – so in the short to intermediate time scales not performing very well but perhaps recovering in the long-term. Thus, my point is that a perspective of higher diversity=higher performance is overly simplistic and should not be advocated or used to produce “maps of resilience”, because these may misdirect the conservation and management efforts.

A technical (but somehow conceptual too) point is the use of traits that may be only indirectly linked to the responses to droughts. Although authors included a light justification for the use of these traits, they haven't got into the needed explanation of the connections of them to the hydraulic traits and the building of functional whole-plant strategies (and there is wide literature available for that, since at least Reich 2014 up to Oliveira 2021). Related to this, it seems incorrect to use groups of traits to access the changes in biomass, instead of the integrated set of traits that may come closer to represent plant strategies related to the way they deal with water, as discussed in the papers I mentioned above.

Reich, P. B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

Oliveira, R. S., Eller, C. B., Barros, F. de V., Hirota, M., Brum, M., & Bittencourt, P. (2021). Linking plant hydraulics and the fast-slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist*, 230(3), 904–923. <https://doi.org/10.1111/nph.17266>

The last point that authors took lightly was the relevance of other determinants of water stress to plants. Even if they do not include the relevant predictors in their analyses, these need to be at least recognized. Beyond water input (precipitation) and loss (evapotranspiration), water in terrestrial systems pass through the soil and ends in the groundwater. Both the properties of the soil (these included in the re-analysis) and the depth to the groundwater (not included) strongly affect plant access to water and thus their responses to droughts (below is a small list of relevant sources, and the last one has an extensive review).

Fan Y. 2015. Groundwater in the earth's critical zone: relevance to large-scale patterns and processes. *Water Resources Research* 51: 3052–3069.

Chitra-Tarak R, Riotte J, Suresh HS, Sean M. 2018. The roots of the drought: hydrology and water

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uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology* 106: 1495–1507.

Sousa TR, Schiatti J, Coelho de Souza F, Esquivel-Muelbert A, Ribeiro IO, Emilio T, Pequeno PACL, Phillips O, Costa FRC. 2020. Palms and trees resist extreme drought in Amazon forests with shallow water tables. *Journal of Ecology* 108: 2070–2082.

Esteban EJJ, Castilho CV, Melgac_o KL, Costa FRC. 2021. The other side of droughts: wet extremes and topography as buffers of drought negative effects in na Amazonian forest. *New Phytologist* 229: 1995–2006.

Roebroek CTJ, Melsen LA, van Dijke AJH, Fan Y, Teuling AJ. 2020. Global distribution of hydrologic controls on forest growth. *Hydrology and Earth System Sciences* 24: 4625–4639.

Costa, F. R. C., Schiatti, J., Stark, S. C., & Smith, M. N. (2022). The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? *New Phytologist*. <https://doi.org/10.1111/nph.17914>

A point I didn't noticed before is that results pointing that forests experiencing larger biomass loss are those with lower functional diversity may be only a consequence of these being the drier forests where changes in water stress were larger, and may not relate directly to the diversity itself. It doesn't seem that the proper controls in the analyses were used to assure that this is not just a circular result.

Here some minor points that may help improve the text:

L 60-62. But if these forests, as shown by this own research, are less able to cope with drought, how conserving them would help? Formal conservation actions (such as setting reserves) don't change the climatic drivers, so I don't see how these actions would be effective. I suggest this sentence to be substituted by a clear statement on how to help these forests in face of their likely higher sensitivity. In my opinion (but this is just my opinion) conservation needs to go beyond the conservation of ecosystems with present-day value, and target the ones with higher resilience in the projected future.

L72-74. this prediction has been formulated several years ago by ecosystem ecologists. Would be interesting to rescue that and show that here you are potentially unveiling the reason behind those predictions.

L89-91. As argued before, there is more determinants of water stress than climate. See <https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.17914>

L11-115. redundancy in itself is not the relevant property, but how close the redundant trait values are to the optimal values required under some environ change

L129-131. the link between these traits and the hydraulic traits directly relevant to responses to droughts need to be established to underscore these affirmations and provide the correct context. See: doi: 10.1111/nph.17266



L141. CEC is not the best indicator of soil fertility, since it includes Aluminum, which is not a nutrient and is actually toxic to plants. This a metric relevant to agriculture more than to forest ecology (see a discussion in Moulatlet et al. 2017). A recognition of this point is necessary.

Moulatlet, G. M., Zuquim, G., Oliveira, F., Figueiredo, G., Lehtonen, S., Emilio, T., ... Tuomisto, H. (2017). Using digital soil maps to infer edaphic affinities of plant species in Amazonia : Problems and prospects. (March), 1–15. <https://doi.org/10.1002/ece3.3242>

L157. why would soil conditions in wet forest be more stable or favorable than in dry forests?
wet conditions may actually lead to leached and less stable soils.

L169-170. every trait does play a role... The real point is how they combine to form the strategies leading to certain pattern of growth survival etc. This reasoning has not yet been built into the ms

L183-184. what is the point of running a pca of 4 variables?

L194-196. results seem mixed up here, as the paragraph started by stating those were responses to the mean historical MCWD

L200-202. these lines should be better kept together with the next paragraph

Fig1 and 2. legends to the y axes need to be described (takes a while to realize what NU, Pho and MO are). The actual data points are missing from the figures. There shouldn't be results figures without the actual data, since this precludes readers evaluating the distribution and dispersal of values

L265. the maps only spatialize what models detected, so this is repeating the results from above.
Would be better to point the spatial (geographical) patterns.

L306. I think that these calculations should be restricted to the combined map, since this is where at least the combination of traits may be representing an approximation of strategies that may relate to the actual traits relevant to understand responses to drought.

L316-318. Forests are not entities seeking to achieve goals, so to say that "forests maximize FD" is not correct.

Reviewer #4 (Remarks to the Author):

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Overall, the authors have done a thoughtful and detailed revision. They have combined comments from four reviewers and made the manuscript more understandable now. The more detailed table and figure captions help a lot, as does some of the clarity in the language. For the most part I am satisfied with the job that the authors have done.

I am not quite sure I agree with your reasoning on not replacing functional diversity with functional dispersion (it's being more precise), but I will concede on that point. In addition, I wish that more information about the species and families were in this paper, but I respect the authors reasons for not including it.

Somewhere in the manuscript can you clarify that in high species richness systems you can have both a lot of functional complementarity and redundancy (with many species you can the complementarity but you can also gain the redundancy). This could perhaps go in the second paragraph of the Discussion. In other words, point out when things are not mutually exclusive.

I appreciate the revisions made. Very interesting results, and the maps tell a compelling story.

*****END*****

Author Rebuttal, first revision:



Response to Reviewers from manuscript (NATECOLEVOL-210914541A):

Functional susceptibility of tropical forests to climate change

Aguirre-Gutierrez, Jesus, Berenger Erika, Oliveras, Imma et al.

Reviewer #1

I believe the authors did a good job reviewing the manuscript and the manuscript has improved a lot. In this second round of review, I raised some points that were not clear or could be improved before publication.

Response:

We thank the reviewer for dedicating time to review our manuscript and below we respond to its comments point-by-point. We believe that based on the new reviews we have improved the clarity of our analysis and general manuscript.

R1-1: In your response to R2-2, if I understand correctly, you mentioned that delta AGB was actually relative delta AGB %, but in the manuscript it's still delta AGB. Have you used raw or relative delta AGB?

Response:

We used delta AGB and not delta % Change as described in the manuscript. We did not update the response adequately but we clarify this now in our response. The main text is however correct.

R1-2: The slopes in the Figure 6 are the interaction slopes instead of the slopes, it may confuse some readers. I suggest to make clear that the slope values in the figures are not the slope of the variables of the X axis, but the slope of the interactions between the variables in the X axis and the moderator.

Response:

As requested we have included the clarification of the slopes in the main text in lines 368-370.

R1-3: Regarding the response for R1-4, I appreciated that the authors recognized this limitation in the discussion. However, I would suggest to add a statement in the introduction and/or methods recognizing that these relationships are proxies of the effects of climate change on FD and that this limitation exists. More specifically, I believe that this limitation is very important and should be mentioned at least in the materials and methods when the context is introduced.

Response:

As suggested we have highlighted this limitation when we introduce the context of the research just before the results section. The new text is in lines 148-150. We expect that these new lines, together with our older text highlighting this limitation also in the discussion would make it clear to the reader that we do not have information on the contemporary changes of FD and FRed.

R1-4: In the responses for R1-5 and R1-6 the authors have not mentioned what they think about using the relative values of delta AGB. I am even more confused because of their response to R2-2 where they mentioned the % delta AGB. Could the authors show the correlation between % and raw changes in AGB?



Response:

We left a previous version of the response in our last document, the response should have stated we used delta AGB and not delta % AGB, however, this is correctly specified in our main text. Given that delta AGB and delta % AGB are significantly highly correlated we decided to work with the former. We used delta AGB as well as the reader can see directly the amount of change in AGB in the original units (Mg C ha^{-1}) and thus get a clearer idea of the change that occurred. The correlation result is shown below:

Pearson's product-moment correlation

data: AGB change vs AGB relative change

$t = 16.122$, $df = 84$; $p\text{-value} < 2.2\text{e-}16$; 95 percent confidence interval: 0.80, 0.91

Correlation: 0.87

Reviewer #2

The authors have extensively responded to the comments made by the reviewers and have incorporated most of the suggestions that were made. Therefore, they have absolved any concerns I had. I think this would be a great paper for the readers of Nature Ecology and Evolution. I only have 3 minor comments:

Response:

We thank the reviewer for its comments, below we respond to each one of them and highlight the changes made in the manuscript.

R2-1: l. 118, maybe replace substituting by compensating? Substitutes seem that the species was not having that role before?

Response:

We have changed the word as suggested.

R2-2: l.435-437 Enso causes anomalous high precipitation in tropical coastal areas so better specify droughts are observed in tropical rainforest.

Response:

We modified the text to state 'tropical forests' instead of 'tropical regions'.

R2-3: l. 478-479 Is something is wrong with this sentence (grammar)?

Response:

We updated the text as follows: 'Across the tropics a diverse set of climatic conditions support'...

Reviewer #3

Dear authors,

R3-1: I see that you have worked on some of the major technical issues, e.g. the inclusion of soil layers, which indeed proved relevant as me and another reviewer have indicated. However, I also see that you have taken some conceptual and technical points too lightly, which in my perspective weaken this contribution.



Response:

Dear reviewer, we thank you for taking the time to review our manuscript and for your relevant comments which we have taken extremely seriously and to which we respond in a point-by-point bases below.

R3-2: The conceptual point is the theoretical basis for the use of FD and Fred in the prediction of ecosystem susceptibility to change. Although the published literature posit the hypothesis that higher functional diversity should lead to higher ecosystem resistance/resilience, through the insurance effect, this hypothesis lacks important parameters: where the system starts (in terms of the traits mean and amplitude), the intensity and direction of the environmental change, and the time scale.

Response:

We totally agree with the point made. The functional diversity and insurance hypothesis, which has been presented and reported upon by several peer-reviewed work (e.g. Yachi et al. 1999; Valone et al. 2008; Shanafelt et al. 2015; Cadotte et al. 2012; Loreau et al. 2021), poses the expectation that more diverse communities may have higher chances of maintaining their state, i.e. not transitioning between alternative states such as from tropical forests to savanna vegetation, in face of environmental change impacts, such as droughts, than less diverse communities.

-Yachi, Shigeo, and Michel Loreau. "Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis." *Proceedings of the National Academy of Sciences* 96.4 (1999): 1463-1468.

-Valone, Thomas J., and Nicholas A. Barber. "An empirical evaluation of the insurance hypothesis in diversity–stability models." *Ecology* 89.2 (2008): 522-531.

-Shanafelt, David W., et al. "Biodiversity, productivity, and the spatial insurance hypothesis revisited." *Journal of Theoretical Biology* 380 (2015): 426-435.

-Cadotte, Marc W., Russell Dinnage, and David Tilman. "Phylogenetic diversity promotes ecosystem stability." *Ecology* 93.sp8 (2012): S223-S233.

-Loreau, Michel, et al. "Biodiversity as insurance: from concept to measurement and application." *Biological Reviews* 96.5 (2021): 2333-2354.

R3-3: A functionally diverse community with trait means and amplitude very far from that required to cope to the intensity of the change can be expected to have a much poorer response (and eventually totally collapse) than a community whose traits are less diverse but close to those required to deal with the new conditions. A community in between (with some functional diversity, but still not too close to the direction of change) can be expected to have some elements surviving (those with adequate traits for the new conditions) – so in the short to intermediate time scales not performing very well but perhaps recovering in the long-term.

Response:

We find it imperative that when testing the hypothesis mentioned above the research makes it clear in which system it is being tested and what aspect of changing climate is being addressed. For instance perhaps it would not be so straightforward to compare tundra vegetation responses to a changing climate versus tropical forests and systems within them therein. In our analysis we make sure to clarify that the system we are comparing is tropical forests and the drivers of change across the system are the same. Within the tropical forests we compare we have gradients of diversity and of climate. Having the ecosystem and drivers of change in mind as suggested above then we could expect that under the same climate change circumstances plant communities that are more diverse may, probabilistically speaking, have higher chances of adaptation to the new conditions given they have within the species/traits values pool a range of them that may deal well with the new climatic conditions (e.g. a drop in water availability of 500 mm in comparison to the common average).



Again, such large species/traits values pool is larger in this given system because conditions (e.g. water availability, soil) are better for diversification and provide more available niches for different species with different trait values than in locations with worst/selective climate and soil conditions (e.g. in the case of plants). In this last system the diversity/trait values range is expected to be lower than in the one with better climatic and soil conditions. Thus a drop of 500mm water in the first system may eliminate some species but may leave many others that can deal with the drought, however, in the second system it is probable it would have lower chances of adapting to the new conditions as it already has a narrow species /traits ranges pool and also because the few species adapted to the original conditions may be at their physiological limits of adaptations to what is already a harsh environment (drier environments), so that further decreases in water availability by another 500mm would be devastating.

At respect of the theory and hypothesis highlighted above Allen et al. (2017) have also recently discussed if systems already adapted to dry conditions in tropical forests may deal better with further droughts (a changing climate) than wetter tropical forests. We have tested the above in West Africa where a long-term drought has been going on for the last decades and where we demonstrate that while wetter tropical forests are not changing much as a response to the increases in drought, it is the drier tropical forests that are changing the most and becoming more homogenous across time (e.g. Fauset et al. 2012, Aguirre-Gutierrez et al. 2019 and 2020). It is also evident, as shown by recent research, that in the Amazon forest a similar pattern of changes is occurring (Esquivel-Muelbert et al. 2019).

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C. et al. (2017). Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environ. Res. Lett.*, **12**, 023001.

Fauset, Sophie, et al. "Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana." *Ecology letters* 15.10 (2012): 1120-1129.

Aguirre-Gutiérrez, Jesús, et al. "Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity." *Nature communications* 11.1 (2020): 1-10.

Esquivel-Muelbert, Adriane, et al. "Compositional response of Amazon forests to climate change." *Global Change Biology* 25.1 (2019): 39-56.

Aguirre-Gutiérrez, Jesús, et al. "Drier tropical forests are susceptible to functional changes in response to a long-term drought." *Ecology Letters* 22.5 (2019): 855-865.

R3-4: Thus, my point is that a perspective of higher diversity=higher performance is overly simplistic and should not be advocated or used to produce "maps of resilience", because these may misdirect the conservation and management efforts.

Response:

We do not suggest that higher diversity equals higher performance, this would perhaps depend on the system and the 'performance' metric. However, we suggest that communities that are more functionally diverse and functionally redundant may have a wider range of trait values, which in turn may allow species to adapt to the new climatic conditions and thus avoid a transition towards an alternative state.

We do not show 'maps of resilience' and we do not call them that way as this may prove equivocal. Along the manuscript we present the theory on the possible link of functional diversity and



functional redundancy and ecosystem resilience. Then, we present spatially explicit models of such diversity and redundancy scores. Only then, and after introducing the theory behind functional diversity, redundancy and resilience and having shown the predicted models, we discuss the maps as ‘potential’ guides to look at when investigating forest resilience.

Taking into account comments 2 to 4 from the Reviewer we now include in the discussion section text that highlights the need for caution when interpreting the functional diversity and redundancy maps and also around inferences made from the functional diversity/redundancy and possible resilience. The new text is in lines 381-386:

‘...Here we provide spatially explicit models of forest functional diversity and functional redundancy that may aid on this endeavour. However, such predictions may not directly reflect the actual resilience of forest towards climate change as other biological (e.g. competition, dispersal) and climatic (e.g. ground water depth, microclimate) may also play a pivotal role on the responses of tropical forests to a changing environment.’

R3-5: A technical (but somehow conceptual too) point is the use of traits that may be only indirectly linked to the responses to droughts. Although authors included a light justification for the use of these traits, they haven’t got into the needed explanation of the connections of them to the hydraulic traits and the building of functional whole-plant strategies (and there is wide literature available for that, since at least Reich 2014 up to Oliveira 2021). Related to this, it seems incorrect to use groups of traits to access the changes in biomass, instead of the integrated set of traits that may come closer to represent plant strategies related to the way they deal with water, as discussed in the papers I mentioned above.

Reich, P. B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

Oliveira, R. S., Eller, C. B., Barros, F. de V., Hirota, M., Brum, M., & Bittencourt, P. (2021). Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist*, 230(3), 904–923. <https://doi.org/10.1111/nph.17266>

Response:

Given the extensiveness of our literature review in what concerns the relationship of the selected plant traits and a changing climate (table S2) we demonstrate we do not take this issue lightly; on the contrary we believe it is a pivotal issue for discussion. We are also aware of the fantastic work published by Peter Reich and Rafael Oliveira, especially those two manuscript cited above. We know they highlight the importance of hydraulic traits such as hydraulic safety margin, P50, root hydraulics, leaf water status, but also of other traits such as leaf phenology, leaf area, LMA and leaf nutrients and photosynthesis. They also discuss certain associations between these traits, from which it is great to learn about the important role that hydraulic traits play for plant adaptations to drought.

In our study, although it would had been great to have access to hydraulic traits across the tropics for all the species we analysed, we are not addressing the relationship between hydraulics and droughts. As described in our Table S1, with peer reviewed work, there are other sensitive plant traits that hold a relationship with a changing climate and for which we have put an offer to collect them across the four tropical continents.

In relation to the comment on groups of traits: plant communities may be composed of species with different life strategies, which may vary (or not) from tropical forest to tropical forest. While it would be an option to work with ‘hypothesise strategies’ across tropical forests, this runs the risk of generating more noise into the analysis in case the ‘hypothesised strategy’ does not represent the



strategies in the actual system or the specific forest community. Therefore, we made the decision of grouping the traits based on what they represent following up to date literature and this is how the morphological/structural, leaf chemistry and photosynthetic traits groups were formed. In our work we are quantifying how different groups of related functional traits explain biomass change after droughts. If the selected functional groups would not have any relation with the changes in biomass we would expect to see no relationship between these two. However we show that different trait groups each can partially explain observed changes in AGB even if these traits are not purely hydraulic. We think that some functional traits, although not being classified as hydraulic traits, can also help understanding the effect of drought on tropical forest ecosystems (see Table S2 for our list of relevant references).

We have now included reference to the work of Oliveira et al. 2022 and Reich 2014 when discussing the importance of hydraulics traits in our manuscript and have further developed this as a paragraph in which we discuss further the link between hydraulics and leaf-wood economics traits in lines 483-505:

‘We also highlight the need for measuring more widely other plant functional traits that have a more direct link to the availability, accessibility and transport of water resources and to adaptations to a drying climate such as plant hydraulic traits (e.g. vessel density, P_{50} , hydraulic safety margin, hydraulic conductivity, osmotic potential, root size and depth) which are seldom available for most tropical plant species but that may shed more light into the possible responses of tropical forest to a changing climate^{53, 54}. However, recent work has shown there is strong correlation between plant hydraulics and economic traits. For instance wood density may serve as a proxy for hydraulic traits⁵⁵ and has been shown to correlated with vessel diameter, branch and tree leaf specific conductivity^{56, 57, 58}, resistance to embolism^{57, 59}, sapwood capacitance^{60, 61}, minimum leaf water potential⁶² and leaf water potential at turgor loss⁶⁰. Also, significant relationships between SLA and conduit diameter, seasonal change in pre-dawn leaf water potential and stomatal conductance have been found⁶², together with significant correlation between leaf P_{50} and leaf mass per area (LMA) and leaf hydraulic conductivity and LMA⁶³. Moreover, the leaf osmotic potential at full turgor and leaf nitrogen content have been shown to be largely correlated⁶⁴. Given that within the hydraulics traits, and thus their leaf and wood economics correlates, and in face of a changing environment, there is a trade-off involving drought avoidance and hydraulic safety. Such trade-off forms an important axis of variation across tropical forests where it is expected that fast-growing species have lower hydraulic safety compared to slow-growing species⁵⁴. Across the tropics species that can quickly transport water resources would tend to be the ones with low wood density, short leaf life span and high rates of resources acquisition⁵³. We expect this relationship to scale up from the individual to the ecosystem level and that this is thus reflected in ecosystem characteristics such as above ground biomass.’

R3-6: The last point that authors took lightly was the relevance of other determinants of water stress to plants. Even if they do not include the relevant predictors in their analyses, these need to be at least recognized. Beyond water input (precipitation) and loss (evapotranspiration), water in terrestrial systems pass through the soil and ends in the groundwater. Both the properties of the soil (these included in the re-analysis) and the depth to the groundwater (not included) strongly affect plant access to water and thus their responses to droughts (below is a small list of relevant sources, and the last one has an extensive review).

Fan Y. 2015. Groundwater in the earth’s critical zone: relevance to large-scale patterns and processes. *Water Resources Research* 51: 3052–3069.



Chitra-Tarak R, Riotte J, Suresh HS, Sean M. 2018. The roots of the drought: hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology* 106: 1495–1507.

Sousa TR, Schietti J, Coelho de Souza F, Esquivel-Muelbert A, Ribeiro IO, Emilio T, Pequeno PACL, Phillips O, Costa FRC. 2020. Palms and trees resist extreme drought in Amazon forests with shallow water tables. *Journal of Ecology* 108: 2070–2082.

Esteban ELL, Castilho CV, Melgac_o KL, Costa FRC. 2021. The other side of droughts: wet extremes and topography as buffers of drought negative effects in na Amazonian forest. *New Phytologist* 229: 1995–2006.

Roebroek CTJ, Melsen LA, van Dijke AJH, Fan Y, Teuling AJ. 2020. Global distribution of hydrologic controls on forest growth. *Hydrology and Earth System Sciences* 24: 4625–4639.

Costa, F. R. C., Schietti, J., Stark, S. C., & Smith, M. N. (2022). The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? *New Phytologist*. <https://doi.org/10.1111/nph.17914>

Response:

We agree there may be many other water related variables that may have an impact on the distribution of tropical forests and their response to droughts. In our analysis we selected relevant predictors and proxies of water availability effects on plant distributions, survival and persistence, such as MCWD and VPD. During our variables selection we had to be pragmatic and select only covariates that besides been relevant for our study also had spatially explicit predictions (i.e. maps) that we could use when predicting FD and FRed across the tropics, something that is not available for some relevant variables such as the water table depth. However, we understand the point of the reviewer about highlighting this issue and we have updated our text accordingly in lines 625-638:

‘There are other possibly relevant predictors of water stress for plants in tropical forests such as the water table depth^{17,81}. It has been hypothesised that water table depth drives the distribution of plant species and functional composition, and where it is expected that forest in shallow water table areas show higher mortality during strong drought events (e.g. El Niño) given the presence of species with shallower roots and less adapted traits^{17,81}. However, we did not include the water table depth in our analysis given the lack of spatially explicit predictions across the tropics.’

R3-7: A point I didn’t noticed before is that results pointing that forests experiencing larger biomass loss are those with lower functional diversity may be only a consequence of these being the drier forests where changes in water stress were larger, and may not relate directly to the diversity itself. It doesn’t seem that the proper controls in the analyses were used to assure that this is not just a circular result.

Response:

This is a good point; however this is not the case as we show in Figure 6 and Table S2 that changes in water availability (small to large) occurred along the functional diversity space, i.e. they were not conditioned to either extreme of the functional space or AGB gradient.

R3-8: Here some minor points that may help improve the text:



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L 60-62. But if these forests, as shown by this own research, are less able to cope with drought, how conserving them would help? Formal conservation actions (such as setting reserves) don't change the climatic drivers, so I don't see how these actions would be effective. I suggest this sentence to be substituted by a clear statement on how to help these forests in face of their likely higher sensitivity. In my opinion (but this is just my opinion) conservation needs to go beyond the conservation of ecosystems with present-day value, and target the ones with higher resilience in the projected future.

Response:

This is a great observation and based on it we have improved our text in lines 60-62:

'Global actions to conserve tropical forests could be enhanced by having local knowledge on the forests functional diversity and functional redundancy as proxies for their capacity to respond to global environmental change.'

And this is also something we have already in lines 516-522:

'From the ecosystems conservation point of view, it is of critical importance to inform decisions by mapping tropical regions in terms of their resilience to future changes in the environment. Conservation efforts need to prioritise and manage ecosystems accordingly, especially including drier tropical forests in the conservation agenda, but also considering that wet tropical forests with higher functional diversity and higher functional redundancy are likely to continue to be long term carbon stores and be more resilient in the face of climate extremes and pathogens.'

R3-9: L72-74. this prediction has been formulated several years ago by ecosystem ecologists. Would be interesting to rescue that and show that here you are potentially unveiling the reason behind those predictions.

Response:

We agree and this is what we have been showing in our recent work (Aguirre-Gutierrez et al, 2019 Ecol. Lett.; Nat. Comms. 2020) and in lines 429-460.

R3-10: L89-91. As argued before, there is more determinants of water stress than climate. See <https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.17914>

Response:

We agree there are other relevant metrics such as the water table depth described in the manuscript suggested above and cite it now in lines 92-93. We did not include this metric as there is no pantropical estimate of it but would be great if this would become soon available.

R3-11: L11-115. redundancy in itself is not the relevant property, but how close the redundant trait values are to the optimal values required under some environ change

Response:

Both redundancy and diversity are relevant properties in this study. This comment is highly related to those from comment 2 to 5 and their responses and therefore direct the reviewer to see our responses to those.

R3-12: L129-131. the link between these traits and the hydraulic traits directly relevant to responses to droughts need to be established to underscore these affirmations and provide the correct context. See: doi: 10.1111/nph.17266

Response:

We agree and we have done this along lines 483-505 also based on the comment five above.



R3-13: L141. CEC is not the best indicator of soil fertility, since it includes Aluminum, which is not a nutrient and is actually toxic to plants. This is a metric relevant to agriculture more than to forest ecology (see a discussion in Moulatlet et al. 2017). A recognition of this point is necessary. Moulatlet, G. M., Zuquim, G., Oliveira, F., Figueiredo, G., Lehtonen, S., Emilio, T., ... Tuomisto, H. (2017). Using digital soil maps to infer edaphic affinities of plant species in Amazonia : Problems and prospects. (March), 1–15. <https://doi.org/10.1002/ece3.3242>

Response:

We have included this point in lines 635-638: ‘Although the CEC includes the acid aluminium, which is not a plant nutrient and may be toxic to plants, this is one of the best estimates of the overall potential of the soil to exchange cations (Ca, Mg, and K) that is available at a pantropical extent.’

R3-14: L157. why would soil conditions in wet forest be more stable or favorable than in dry forests? wet conditions may actually lead to leached and less stable soils.

Response:

We certainly agree with the reviewer in the point of the soils and we have modified the text so it refers to climate and not soil.

R3-15: L169-170. every trait does play a role... The real point is how they combine to form the strategies leading to certain pattern of growth survival etc. This reasoning has not yet been built into the ms

Response:

Perhaps this point is a repetition from point five above. There are different strategies that may work in different locations with different environmental conditions and certainly more than one strategy can be successful in the same location. Thus the scope of this manuscript is not to elucidate each one of these strategies and how they combine in the ecosystem. However, we have certainly included vast background information in our Table S2 and in the main text (also taking comments 2-5 into account) in lines 483-505 so the reader can form its own opinion about our findings and about the role that the functional traits we use have as means of adaptations to a changing climate.

R3-16: L183-184. what is the point of running a pca of 4 variables?

Response:

Elucidate the distribution of the data in the first two main axes that drive the patterns observed.

R3-17: L194-196. results seem mixed up here, as the paragraph started by stating those were responses to the mean historical MCWD

Response:

They are not mixed, first we starting by describing the effects of MCWD and then move on describing the effects of the other covariates in the model as shown by Figure 1.

R3-18: L200-202. these lines should be better kept together with the next paragraph

Response:

We have moved those lines to the next paragraph as suggested.

R3-19: Fig1 and 2. legends to the y axes need to be described (takes a while to realize what NU, Pho and MO are). The actual data points are missing from the figures. There shouldn't be results figures



without the actual data, since this precludes readers evaluating the distribution and dispersal of values

Response:

We have now included descriptions of the X and Y axis in figures 1 and 2. To show variation in the model outcome based on the data used to fit the models (here called data points by the reviewer) we show the grey fitted lines. This is a better way to show variation in the model and data than just showing the raw points used, which if were included (the points) would also make the graph look too crowded making it difficult to understand.

R3-20: L265. the maps only spatialize what models detected, so this is repeating the results from above. Would be better to point the spatial (geographical) patterns.

Response:

We agree, and that is what we do in lines 280-297 and 312-327. We included that explanation to which the reviewer is referring to (old line 265 onwards) by the request of another reviewer.

R3-21: L306. I think that these calculations should be restricted to the combined map, since this is where at least the combination of traits may be representing an approximation of strategies that may relate to the actual traits relevant to understand responses to drought.

Response:

We think it is highly useful for the reader to understand the core results by it being able to understand the distribution of the FD and FRed for each one of the traits used separately, which actually form the basis of the combined map.

R3-21: L316-318. Forests are not entities seeking to achieve goals, so to say that "forests maximize FD" is not correct.

Response:

Following the comment from the reviewer we have updated the text as follows: 'The bivariate FD-FRed predictions show that most tropical forests across West Amazon and Central Africa reach some of the highest predicted morphological and photosynthesis FD and FRed, while a smaller area of western South America reaches some of the highest predicted nutrients FD and FRed (Fig. 5).'

Reviewer #4

Overall, the authors have done a thoughtful and detailed revision. They have combined comments from four reviewers and made the manuscript more understandable now. The more detailed table and figure captions help a lot, as does some of the clarity in the language. For the most part I am satisfied with the job that the authors have done.

Response: We thank the reviewer for going through the manuscript one more time and for the comments below, which we address here and in the main manuscript.

R4-1: I am not quite sure I agree with your reasoning on not replacing functional diversity with functional dispersion (it's being more precise), but I will concede on that point. In addition, I wish that more information about the species and families were in this paper, but I respect the authors reasons for not including it.



Response: Thank for understanding our points and deciding it is fine to leave the terms functional diversity and not include the species list in the text.

R4-2: Somewhere in the manuscript can you clarify that in high species richness systems you can have both a lot of functional complementarity and redundancy (with many species you can the complementarity but you can also gain the redundancy). This could perhaps go in the second paragraph of the Discussion. In other words, point out when things are not mutually exclusive.

Response:

We have included the text suggested by the reviewer in lines 389-390 of the main text.

R4-3: I appreciate the revisions made. Very interesting results, and the maps tell a compelling story.

Response:

We thank the reviewer for its constructive comments across the revisions made.



Decision Letter, second revision:

28th February 2022

Dear Dr. Aguirre Gutierrez,

Thank you for submitting your revised manuscript "Functional susceptibility of tropical forests to climate change" (NATECOLEVOL-210914541B). It has now been seen again by the original reviewer 1, who is fully satisfied (they had no remaining comments for authors). Reviewer 3 was unavailable to re-review but we felt satisfied that we could proceed. We are be happy in principle to publish your paper in Nature Ecology & Evolution, pending minor revisions to comply with our editorial and formatting guidelines.

If the current version of your manuscript is in a PDF format, please email us a copy of the file in an editable format (Microsoft Word or LaTeX)-- we can not proceed with PDFs at this stage.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution. Please do not hesitate to contact me if you have any questions.

[REDACTED]

Our ref: NATECOLEVOL-210914541B

7th March 2022

Dear Dr. Aguirre Gutierrez,

Thank you for your patience as we've prepared the guidelines for final submission of your Nature Ecology & Evolution manuscript, "Functional susceptibility of tropical forests to climate change"

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(NATECOLEVOL-210914541B). Please carefully follow the step-by-step instructions provided in the attached file, and add a response in each row of the table to indicate the changes that you have made. Please also check and comment on any additional marked-up edits we have proposed within the text. Ensuring that each point is addressed will help to ensure that your revised manuscript can be swiftly handed over to our production team.

****We would like to start working on your revised paper, with all of the requested files and forms, as soon as possible (preferably within two weeks). Please get in contact with us immediately if you anticipate it taking more than two weeks to submit these revised files.****

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In recognition of the time and expertise our reviewers provide to Nature Ecology & Evolution's editorial process, we would like to formally acknowledge their contribution to the external peer review of your manuscript entitled "Functional susceptibility of tropical forests to climate change". For those reviewers who give their assent, we will be publishing their names alongside the published article.

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[REDACTED]

Reviewer #1:
Remarks to the Author:
-

Final Decision Letter:

24th March 2022

Dear Dr Aguirre Gutiérrez,

We are pleased to inform you that your Article entitled "Functional susceptibility of tropical forests to climate change", has now been accepted for publication in Nature Ecology & Evolution.

Over the next few weeks, your paper will be copyedited to ensure that it conforms to Nature Ecology and Evolution style. Once your paper is typeset, you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required

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Due to the importance of these deadlines, we ask you please us know now whether you will be difficult to contact over the next month. If this is the case, we ask you provide us with the contact information (email, phone and fax) of someone who will be able to check the proofs on your behalf, and who will be available to address any last-minute problems . Once your paper has been scheduled for online publication, the Nature press office will be in touch to confirm the details.

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