Response to the editor

I have now received two very constructive reviews, both liked components of your manuscript but both raised a number of important issues that need to be carefully revised before this manuscript can be considered for publication.

In particular, the highlighted the sampling bias issue, which will need to be discussed very clearly in the revised text. I think adding text discussing a sensitivity test to the assumed drought thresholds is warranted. R1 highlighted the problematic nature of the author's drought threshold which leads to non-physical oscillating drought/non-droughts. This also likely leads to a gross over-estimate of drought occurrence too? Would it make sense to compare to something like SPI, which can be used to better integrate month-to-month behaviour. R1 highlighted your VPD range, which you've now fixed, I think it would be good to show that the new estimated values are consistent with any flux records you have in a supplementary figure to satisfy a reader. Both reviewers commented on a general lack of clarity in your methods, please carefully revise this.

Response: thank you for allowing us to revise our manuscript and for your careful review of the referee comments and our manuscript. Below we will reply point by point (in red) and in detail to the comments and suggestions raised by you and by the two referees. At the end of this document is the revised manuscript with the changes made visible using the “track changes” option in MS Word.

We have made a few major revisions in the analysis and the manuscript following the (shared) comments and suggestions raised by you and by the two referees:

1) the sampling bias issue was indeed raised by both referees and is largely based on a misunderstanding on how the episodic drought months are counted. We have now included a second analysis where we counted the number of episodic drought months per year in a regular 1° grid covering our study area, it shows a similar trend (new Figure S4). By providing more context about the counting of the episodic drought months per year in the Methods, Results and in the Figure captions, we hope that his issue is now resolved.

2) we have now resolved the problem of the timeseries oscillating between wet and dry seasons highlighted by referee #1 by omitting single wet season months when they are in between two dry season months, and vice versa. This has resulted in extended periods of wet season and dry season that better capture the “actual” dry season at which referee #1 was referring to in the report (new Figure 1). This new smoothening method has also made the 65% quantile threshold, which was confusing to both referees, obsolete.

3) we performed a sensitivity analysis by rerunning the meta-analysis using two additional episodic drought thresholds (see Methods). The results of this sensitivity analysis are shown as two additional Figures in the Supplement (Figure S8 and S9).

4) The issue with the VPD has now been fixed, the methodology about retrieving midday VPD has been updated and the comparison of monthly averaged midday VPD from ERA5 with the monthly averaged midday VPD from the flux towers has been included in the Supplement (Figure S1).

I also have a number of key methodological issues that I really am not clear on, in particular the assumptions you make when comparing fluxes, in particular how you're controlling for LAI differences between species? Similarly, you're comparing fluxes that vary diurnally / seasonally / annually, so, how are you control for this to ensure your comparisons are meaningful? Would a maximum stomatal conductance make more sense than a direct measurement of stomatal conductance? If this information was explained, then I apologise - I note you say they are midday values but I don't recall reading this in your paper. I am similarly uncomfortable with the idea that you generate a number of derived metrics (e.g. WUE) from fluxes that are not measured (e.g. transpiration). In your response to R1 you note the use of a linear reln, where was this shown? Your assumption of perfect coupling to get transpiration is likely to be a gross error (see citations below).

I have listed a number of points that I also observed whilst reading through your paper below.

* Can I ask you to check this statement: "Multi-year droughts are defined as a more permanent reduction of precipitation spanning years to decades, as projected by some climate model simulations (Boisier et al., 2015; Malhi et al., 2009)." I'm happy to be proven wrong, but my understanding was that coupled-climate models fail to project multi-year droughts.

Response: we cannot find any references that suggest that multi-year droughts are projected to become more frequent in coupled-climate models. The references to Boisier et al. 2015 and Malhi et al. 2009 are more about dry season lengthening, which we agree is not the same. We have omitted this statement from the revised version.

* Line 100: "aboveground net primary productivity" - why only aboveground? This seems a curious distinction to make, why wouldn't drought also impact below-ground growth?

Response: we chose to use above-ground NPP because monthly estimates of root productivity are very scarce in the neotropics. In the new version of the manuscript we have also included total NPP in addition to ANPP in the meta-analysis.

* Line 124: "as suggested by remote sensing analysis" - it would be good to include a word like "derived" in there, as the estimate of isohydricity from VOD is not a direct measurement. Further, the text at the end of that paragraph sets up a binary: isohydric vs anisohydric, in reality, there is more of a spectrum of behaviour, it would be nice if the text better reflected this.

Response: this sentence is now omitted from the manuscript. We followed the suggestion of referee #2 to omit mentioning the concept of isohydric vs non-isohydric behaviour and focus on the mechanisms instead.

* In your meta-analysis search terms you have "gross ecosystem productivity", does that mean you ignored studies that report gross primary productivity, or Asat?

Response: no, we also used reported values of gross primary productivity, which are used interchangeably in the literature. We now use GPP in the manuscript because it makes more sense comparing GPP and NPP and not GEP and NPP.

* Line 196: technically this is not ANPP, as your estimate is biomass change - turnover of tissues; ANPP is simply a summed growth term. It might be better to describe this as something more aligned with biomass? I realise that the approach you've taken is extremely common in the literature.

Response: this might be a misunderstanding, as also in our calculation ANPP is a summed growth term (stem growth + canopy growth). We have adapted this sentence to also include total NPP and highlight that ANPP and NPP are just a sum of these growth terms.

* It would be good to report in a table how many of these metrics, collected and derived you have for each of the 229 sites. I found myself wanting to see this while reading the methods. It is very clear from looking at your actual database that the collected variables vary considerably across sites. I would like to see the addition of a summary table of some kind with a revised manuscript.

Response: this table has now been added to the Supplement (Table S2).

* I'd prefer you wrote the derived equations you have calculated for your meta-analysis out (with units) in the methods, as it currently isn't clear, e.g. iWUE, WUE, etc. Also, what are these stomatal conductance measurements given that this isn't a static property - how can you compare this across sites if they are measured at different times of day? Is it the maximum stomatal conductance (Gsmax)? If so, please say so. I'm also uncomfortable with you assuming transpiration = gs X D, for an ecosystem known to have leaves that are not well coupled to the boundary layer (see Jarvis and McNaughton 1986; De Kauwe et al. 2017 Biogeosci.). Why not simply constrain your analysis to quantities that you have direct estimates of, as opposed to introducing new assumptions/errors?

Response: we have now added five more equations to the Methods (section 2.2). For all leaf scale measurement (except pre-dawn leaf water potential) we used midday values (~12:00 local time), this was previously not clear but is now highlighted in the Methods (section 2.1, first paragraph). We also more explicitly mention that our estimation of “potential” leaf transpiration is not to be confused with actual leaf transpiration because of the decoupling of atmosphere and leaf boundary layer. Nonetheless, we think that including these derived measures (some of which are simply a ratio of two measures directly retrieved from the literature) still ads value to the meta-analysis of leaf, tree and ecosystem scale responses to drought.

* On a related point, does varying LAI not confound direct comparison between species? How are you controlling for this?

Response: we do not take any measure of leaf area, crown cover or LAI into account into the meta-analysis and we do not directly compare species or individuals. To avoid these sources of uncertainty we have compared study averages of measures, giving the study averaged response to drought. We did this to answer: 1) what is the average response observed across all studies? and 2) can we explain the variability in the responses among studies? All the biases in large or small trees, high LAI or low LAI ecosystems is present in these studies but we did not aim to calculate the absolute response of these measures, just the study averaged response and the average percentage change across all studies. We have included and reformulated a few sentences in the revised version of our manuscript to highlight this difference.

* In the meta-analysis text, you need to be a lot clearer how uncertainty is being estimated across sites. You also need to more clearly describe what you mean "treatment" to be? In some instances, this would be simply wet-season vs dry-season? But what about the experiments that have imposed a manipulation. Are all of these things being compared at once, I didn't find the text clear on these key points.

Response: we have only made two comparisons of natural drought conditions: wet season – dry season and dry season – episodic drought. Therefore the “treatment” in the meta-analysis is either the dry season (and wet season the control) or episodic drought (when dry season is the control).

We have now included two sentences in the Methods (section 2.4, 1st paragraph) in which we explain in more detail what exactly we are comparing.

* "Furthermore, dry season days are often less cloudy resulting in higher net radiation," - where exactly is this statement shown/supported? This may be true, but Fig 2 does not show this.

Response: agree, this is not shown in Figure 2, this statement is now omitted from the Results.

* Fig 2 needs the number of samples/studies above the box-plots.

Response: the number if samples has been included in the new Figure 2.

Response to Referee #1

Janssen et al. examine whether a meta-analysis of leaf-, tree- and ecosystem-level data can help understand, and predict, neotropical rainforest responses to drought. They ask two questions: (i) how does drought impact the vegetation from the leaf to the ecosystem scale?, and (ii) can different hydraulic behaviours at different locations or among species explain differences in the responses to drought? They find that episodic drought effects compound on dry season effects at both the leaf and tree scales. However, vegetation responses are buffered at the ecosystem scale and, notably, are often not significant during episodic drought. Finally, independently compiled wood density data are used to explain some of the variability observed at the leaf and tree scales during the dry season (and to a lesser degree during episodic droughts). I commend the authors for this undertaking (138 studies!) and for the quality of their writing. The study will make an important contribution by explaining the ecophysiological impacts of drought on a key region's rain forests, at a range of scales. However, I have several major methodological concerns that should be addressed in revision.

Response: thank you very much for your extensive report. We appreciate the thorough review of our manuscript and your acknowledgement of the relevance of our work. Below we reply to the comments raised in the referee report and highlight where the changes in the manuscript have been made following your comments and suggestions.

————————————- Main comments ————————————-

My fist observation is that, according to the number of measurements / estimates compiled by the authors, episodic droughts data (624) represent 9% of the total amount of data (6956) and to 17% of the dry season data (3006). This feels like a very high number of episodic drought observations compared to the rest of the observations. Looking at Figure 1b and c, the number of observations per months appears biased towards the more recent years. Does this bias explain the frequency increase in the average of episodic drought months per year in the more recent years?

Response: yes, there is a sampling bias in our meta-analysis towards the more recent years and this does result in more months being classified as episodic drought months than would be expected based on the 10% cut-off point. Furthermore, in this summary we erroneously included multi-monthly data from forest plots that were classified as either episodic drought or dry season months for comparison, these numbers have now been updated. The sampling bias however does not explain the trend of increased episodic drought months per year (Figure 1 b) because the entire time series of ERA5 soil moisture was used to count the episodic droughts at each site, whether we have field data in those months or not (see also specific comment on Figure 1). We have now also included an analysis on the number of episodic droughts per year across the lowland moist neotropical forest biome (new Figure S3 and Table S3) to remove the spatial sampling bias (because of clusters of sites in some places) and find again a significant increase of episodic drought months over the timeseries, together with an increase of midday air temperature and VPD. We hope that in this way we removed all possible confusion for the reader about whether the increase of episodic drought months per year is driven by the increase of months per year with data from the literature (which is not the case).

Looking at Fig. 1d, I am also questioning the definitions used for the wet season, dry season, and episodic droughts. For example, in 2000, the K34 site starts of by being in the wet season for 5 months, then in the dry season for 1 month, then in the wet season again for 1 month, then in the dry season for 2 months, wet season for 2 months, dry season for 1 month, wet season for 2 months, dry season for 1 month.... This pattern of oscillating wet and dry season is seen repeated within the following years, but how likely is it to represent the "real" wet and dry season? And so, how can dry season effects on the vegetation be captured on time scales that make sense?

Response: the separation of months into wet and dry season was indeed based on the depletion or replenishment of ERA5 soil moisture for a specific site. The rationale behind our definition is that when evapotranspiration exceeds precipitation, there is a precipitation deficit resulting in the depletion of soil moisture. This definition is often used to distinguish wet and dry season in neotropical forests and also used to calculate drought metrics such as the cumulated water deficit (Aragão et al., 2007). We have now included a new "smoothening" operation on wet season, dry season classification by labelling a single dry season month in between two wet season months as a wet season month, and vice versa (see Methods 2.3, end of 1st paragraph). This procedure has resulted in longer sequences of months falling in either the wet season or dry season (new Figure 1 d) that make more sense ecologically and it has also made the 65% quantile threshold obsolete.

Again, if we look at the dry season and episodic drought between 2015 and 2016, we see a transition from episodic drought to wet season although the relative extractable soil water is very close to 0. I understand from the authors' definition of the wet season that this is because the soil moisture has started to be replenished. Realistically, if the vegetation had just gone through an episodic drought, then would the next month's measurements of stomatal conductance, photosynthetic rate, etc. be representative of a wet season month? Therefore, owing to potential hydraulic function damage sustained during the drought, the authors might want to rethink their definitions of the wet and dry seasons, as well as of the episodic droughts, in terms of what makes sense when considering potential multi-weeks (but not multi-years) legacy impacts on the vegetation. One solution would be to classify some of the data as being within "recovery months" (i.e. from a drought or from the dry season to the wet season) and to analyse them separately.

Response: on the leaf scale, the available literature reported no clear legacy effects of episodic drought on stomatal conductance, leaf water potential and photosynthesis (Alexandre, 1991; Santos et al., 2018). However, on the tree scale there are legacy effects reported, for example reduced hydraulic conductance and transpiration directly following episodic drought (Fontes et al., 2018) and changes in stem growth and leaf flushing (Doughty et al., 2014, 2015; Hofhansl et al., 2014). We discuss observed legacy effects reported in the literature in the Discussion (L486-L496) and acknowledge that the method used by us is only able to capture instantaneous responses and not the legacy effects, which is a limitation.

The authors should also consider testing the sensitivity of their results to different quantile threshold definitions for what consists in the wet and dry season, as well as in an episodic drought.

Response: the lack of a “sensitivity analysis” was also noted by referee #2 L212-213. In the revised version of the manuscript we have now included as sensitivity analysis (see Methods) and we included the results of this sensitivity analysis in the results (referring to new Figure S8 and S9), and discuss its implications in the Discussion.

My second concern relates to the method used to calculate the percentage changes shown in Figs. 3 and 4. It is very clear from Figs. S2, S3, and S4 that wood density is a good proxy for leaf- and tree-level hydraulic behaviour. So why not cluster the analysis of the rates of change by types of wood density (e.g. low vs high), to ensure that opposite types of leaf- and tree- level behaviours are not compensating and cancelling each other out when looking at the rates of change? I understand that this is what Figs. 5 and 6 attempt to do, but I do think the broader narrative would be more successful had the meta-analysis differentiated between isohydric and anisohydric behaviours from the start. Clustering by behaviour might also help reconciliate and explain the current inconsistencies in the findings from the leaf-level up to the ecosystem scale.

Response: we agree that merging the drought responses of all the species and functional groups present in the database results in the loss of the variability in responses observed. In the case of transpiration this merging indeed results in that we observe on average no significant changes in transpiration from the wet to the dry season (Figure 4) while studies that measured mainly high wood density species or low wood density species did show a significant increase or decrease in transpiration, respectively (Figure 5 and 6). As you mention, showing this variability is the purpose of Figure 5 and 6 while for Figure 3 and 4 the aim is to show the average response. We did consider splitting the data shown in Figure 3 and 4 in studies measuring mainly isohydric and non-isohydric species, however, this distinction is not easily made. As can be seen in Figure 5 and 6, there are not really two clusters of hydraulic behaviour but it is rather a continuum, related to the continuum from strictly isohydric to extreme non-isohydric behaviour that is observed in plants globally (Klein, 2014; Martínez-Vilalta et al., 2014; Meinzer et al., 2017). We think that arbitrary splitting the data in isohydric and non-isohydric studies will not help to reconcile the inconsistencies in drought responses observed from the leaf to the ecosystem scale.

My third point has to do with the VPD values used to estimate changes in leaf level transpiration. The leaf-level transpiration is estimated using the relationship E = gs × D where D is VPD. Here, the authors use monthly averaged atmospheric midday VPD derived from the ERA5 reanalysis data. I am surprised because the VPD values present in the database are very low, with a maximum of 2.35 kPa across all 6956 data points and the 95th percentile < 1 kPa. Given that > 50% of the total data is classified as corresponding to either the dry season or to an episodic drought, I would at least expect the 95th percentile value of the average monthly midday VPD to be > 1 kPa! It is unclear to me whether these low values are due to using the Buck method to calculate VPD, or to the ERA5 data themselves. Additionally, using atmospheric VPD rather than leaf-to-air VPD (which the relation E = gs × D is designed for) ignores feedback effects from the leaf to the atmosphere above. When plants transpire during a drought (or a heatwave), they also cool the air immediately above them, leading to lower leaf-to-air VPD than atmospheric VPD. One finding of this paper is that “the data shows no significant decline in leaf transpiration from the wet to the dry season [. . .] as the average increase of VPD from the wet to the dry season is of the same magnitude as the decline of stomatal conductance”. Instead, higher estimates of midday VPD (e.g. from a different reanalysis product) could lead Janssen et al. to predict an increase in transpiration during the dry season. Or, conversely, using leaf-to-air VPD might lead to a smaller magnitude increase in leaf-to-air VPD than the decline in stomatal conductance, thus leading to predicting a reduction in leaf-level transpiration in the dry *season! It is very hard to tell what the implications of the VPD estimates are, but they currently make it hard to trust the leaf-level estimates of transpiration, Potential ways forward are:*

1. to use a different method than the Buck method and to quantify the uncertainty;

2. to compare the current VPD estimates with different reanalysis products (e.g. ERA-Interim which has been evaluated more) or other products, such as the CRU data, and to quantify the uncertainty;

3. to calculate a proxy of leaf-to-air VPD using atmospheric VPD and leaf water potential to account for a degree of leaf-atmosphere feedbacks.

Response: thank you for pointing out the very low VPD that we used to calculate leaf transpiration in our meta-analysis! After reviewing our pre-processing steps that we used to obtain the ERA5 VPD at every site, we found the mistake that resulted in these low VPD estimates: instead of using local time (12:00) temperature and dewpoint temperature to calculate midday VPD, we erroneously used 12:00 UTC when downloading the ERA5 temperature data. This means that we used early morning VPD instead of midday VPD.

For the analyses in the revised version of the manuscript we now use temperature and dewpoint temperature at four different times (15:00 – 18:00 UTC) that correspond with local 12:00 in four time zones covering our study area (see Methods). The ERA5 results seem to correspond reasonably well with VPD observations from flux towers in our study area (Figure 1). Using the actual midday VPD logically resulted in changes in the range of VPD found in the meta-analysis (Figure 2). However, we observe no major changes in the direction or magnitude of the leaf transpiration response to seasonal and episodic drought (Figure 3). The response of leaf transpiration to seasonal drought remains not significantly different from 0 and significantly declines in response to episodic drought. This can be explained because the new and correct midday VPD is higher compared to the previous VPD estimate in the wet season, in the dry season and during episodic drought which results in marginal changes in the relative response of leaf transpiration.

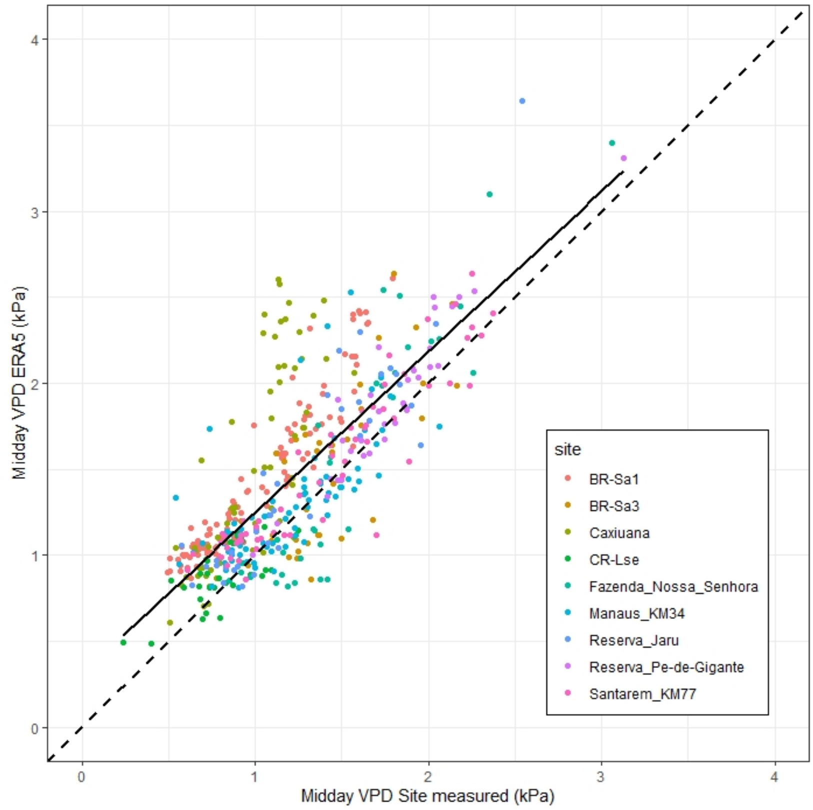

Figure 1 The new ERA5 vapor pressure deficit at midday (12:00) compared with vapor pressure deficit measured at 12:00 at 9 flux tower sites in the study area. The dashed line represents the 1:1 line and the solid line a linear regression fit.

We recognise that atmospheric VPD and leaf-to-air VPD can be very different depending on the cooling feedback resulting from leaf transpiration. However, leaf-to-air VPD, leaf temperature or leaf water potential were not consistently provided in the original source papers that provided the stomatal conductance data, preventing us from calculating actual leaf transpiration. We agree that we have to be more careful with the results from this analysis. In the revised version of the manuscript we now discuss the implications of using atmospheric VPD instead of leaf-to-air VPD in calculating leaf transpiration in the Methods (2.2 1st paragraph).

———————————————- Minor comments ———————————————-

L. 22: it's hard to see how the results could be used as a benchmark for LSMs, given e.g. the unexplained differences in transpiration responses from the leaf and tree- scales to the ecosystem scale. Instead, do the authors mean that the relationships they find between the different variables and wood density could help guide LSM parameterisation efforts in neotropical forests?

Response: yes, we agree with your suggested change of formulation. The new formulation is: "We present new insights into the functioning of tropical forest in response to drought and present novel relationships between wood density and drought responses that can help guide the parametrization of land surface models."

L.32: maybe consider citing Yang et al. 2018 (https://doi.org/10.1038/s41467-018-05668-6), which uses LiDAR and allometric relationships, in place of Zhao and Running? The Zhao and Running paper has temperature dependencies which are problematic and have been discussed in several technical comments....

Response: thank you for your suggested change in referenced literature, Yang et al. 2018 has now replaced Zhao and Running in this references.

L.54: I suggest starting a new paragraph at "Episodic droughts"

Response: this has been changed.

L.55-56: do tropical North Atlantic SST anomalies affect all the neotropics? Or do they primarily affect the easternmost region?

Response: according to Marengo et al. 2011, the North Atlantic SST affected the position of the ITCZ, forcing the ITCZ anomalously northward during 2010, resulting in an episodic drought in the southern Amazon Basin.

L. 75: "stomates progressively close" is more exact than "stomates close"

Response: agree, better formulation. This has been changed.

L.76: also: 1. Martin St-Paul et al. 2017 (http://doi.wiley.com/10.1111/ele.12851), 2. Drake et al. 2017 (https://doi.org/10.1016/j.agrformet.2017.08.026) 3. Choat et al. 2018 (https://doi.org/10.1038/s41586-018-0240-x)

Response: agree, these references are a good addition to Buckley et al. 2019 and have been added.

L. 84-85: E can either stay the same, increase, or decrease during a drought, all of which could result on a decline in Ψl.... Also, ksl declines as a result of a decline in Ψs

Response: thank you for this nice suggestion, the suggestion has now been incorporated into the text and equation 2 has been removed.

L. 87-88: stomatal closure (described above) and stomatal downregulation are not the same, so the link isn't clear from the current phrasing. Also, using the words "potential" and "potentially" could lead to misinterpretation

Response: this sentence has been reformulated.

L. 88-90: Is this meant as a global statement? Or is it still in the context of neotropical forests? Generally, this is quite variable depending on species, ecosystem, and timing... with different responses being observed at different stages of a drought

Response: yes we agree this is confusing, this sentence has been reformulated.

L. 104-106: I think the paragraph would be clearer if this sentence came right after the reference to Sayer et al 2007, L. 102

Response: this has been reformulated.

L. 107: here, maybe repeat what the three spatial scales are

Response: we now repeat the tree spatial scales here.

L. 114: change "drought avoiding and drought tolerating strategies" to "drought avoidance or tolerance strategies"?

Response: this has been reformulated.

L.114-115: xylem embolism doesn't always substantially damage the hydraulic pathway, maybe consider rephrasing as "Drought avoidance strategies aim to avoid dangerous declines in Ψl that could lead to significant xylem embolism and thus damage..."?

Response: yes we agree, this has been reformulated.

L. 118-120: consider rewriting as: "Conversely, drought tolerance strategies imply [. . .] without significant and/or irreversible embolism-induced losses of hydraulic function"?

Response: thank you for the suggestion, this sentence has been adapted.

L. 120-123: the isohydric vs anisohydric (why use "non-isohydric" rather than anisohydric?) need a bit more explanation, e.g. isohydric species maintain a constant midday Ψl but also down-regulate their stomatal conductance. It would also be worth mentioning that the spectrum of isohydric and anisohydric behaviours is quite large, with some species having the capacity to oscillate between more-or-less isohydric or anisohydric behaviours depending on the environmental conditions...

Response: we have omitted all mentions of the isohydric / non-isohydric behaviour following a suggestion by referee #2.

L.131-133: this is a very nice hypothesis! To introduce it, the authors could refer to the work of Rosas et al. 2019 (https://doi.org/10.1111/nph.15684)

Response: thank you, we have restructured this paragraph following a suggestion of referee #2 so that the hypothesis is properly introduced. We use multiple references from neotropical forests to introduce our hypothesis so we see no need to reference the work of Rosas et al. 2019 here.

L. 136-138: I think that moving this sentence to line 133 before "In neotropical..." would make the text flow better

Response: agree, this paragraph has been restructured.

L. 138-140: this is very useful contextualisation, maybe it could make it into the abstract?

Response: we have now included a contextualization in the abstract, mentioning that wood density is not functionally related to plant hydraulic properties but appears to be a good proxy of hydraulic behaviour.

L. 153: typo: "it" to "they"

Response: this has been changed

L. 156: what about measurement techniques and errors? Were those also included in the database? I imagine there would be different margins of error depending on the measurement technique. Also, were there quality checks or did all the above described data make it into the database?

Response: no, we did not differentiate between measurement techniques in the database and this could indeed result in differences in uncertainties. However, since the meta-analysis deals with relative changes in a variable of interest or "effect sizes" the absolute values are less important. Furthermore, since our meta-analysis deals with values that are averaged for the different studies, which each included multiple tree species and individuals, the variability due to differences between species and individuals is much larger compared to measurement uncertainties (see e.g. Santos et al. 2018). It would indeed be very interesting to see how different measurement techniques have an effect on measured drought responses but this is beyond the scope of this study.

L. 157: was the time of day not reported? This would highly impact measurements of stomatal conductance and leaf photosynthesis...

Response: very often the day and time of day were not reported for tree and ecosystem scale responses. For the leaf scale responses (stomatal conductance, photosynthesis and leaf water potential) we always used the value at maximum photosynthesis (at midday), except for pre-dawn leaf water potential, naturally. We have now included this information in the Methods (2.1 1st paragraph) of the revised version.

L. 157-158: how many different species, genus, and/or different site averages?

Response: we refer to the database statistics in the next paragraph and included two new tables (Table S1 and S2) in the supplement to provide the reader with this information.

L. 160-161: the information on how the spatial data were extracted is probably not needed

Response: agree, this has been omitted in the revised version. See also specific comment by referee #2.

L. 171: shouldn't "midday vapor pressure deficit" be "monthly averaged midday vapor pressure deficit"?

Response: yes it should, this has been changed.

L. 173-175: the authors need to mention that this assumption largely ignores variations in root distributions

Response: we have included a sentence about rooting depth in this paragraph.

L. 177-178: please clarify what "ecosystem performance measures" means

Response: the term "performance" was confusing and has been omitted in the revised version of the manuscript.

L. 179: were all the stomatal conductance measurements made at midday? Also, it is worth mentioning that this relationship assumes a perfect coupling between the stomates and the atmosphere above, i.e. it assumes that the boundary layer conductance to water vapour, gb, is much larger than gs. But in forests with large leaves and dense canopies, decoupling is often observed because gb is relatively small, such that when gs and gb are of similar magnitudes E ≈ 0.5 × gs × D. In the context of this study, it is impossible to estimate what the coupling/decoupling factor is at a given location and/or at a given time, but the authors should mention this (in the context of leaf shedding and flushing?), given their findings

Response: we have included two new sentences in this paragraph highlighting the difference between atmospheric VPD and the leaf-boundary layer VPD and how this likely leads to the overestimation of leaf transpiration in our meta-analysis.

L. 184-186: from the text alone, it is very unclear how transpiration was estimated. How does the RMSE represent the linear relationship? Looking at Fig S1, I presume the authors have compiled tree scale measurements of E so, in the analysis, why not just use those measurements (instead of the estimates described by the linear relationship)?

Response: multiple studies that were included in the database reported either maximum sapflux density (at midday) or daily tree transpiration, but not both. We used the linear relationship to calculate daily tree transpiration for the studies that reported only maximum sapflux density. We have now included a new equation and rephrased the sentence to clarify how we derived total daily transpiration from maximum daily sapflux density values reported in the literature.

L. 190: my interpretation of equation 3 is that it should only be valid at steadystate. How did the authors ensure steady-state conditions? Were the data filtered depending on VPD?

Response: yes, equation 3 assumes that the system is at steady state. Steady state conditions were not ensured and we doubt whether we could account for this in a meta-analysis. The "instantaneous soil to leaf hydraulic conductance" calculated here should be regarded a measure of whole-tree hydraulic conductance at midday (Love and Sperry, 2018).

L. 192: typo: "rooting zone" to "root-zone"

Response: this has been corrected.

L. 193-194: strictly speaking, difference between Ψl at midday and $\Psi pre-dawn$ is a proxy of the water gradient within the tree, from the root up to the canopy. For it to equate soil-canopy gradient, further information on tree height would be needed to account for gravitational effects and relate $\Psi pre-dawn$ to Ψs...

Response: yes, this contextualisation has now been added to the sentence.

L. 225-227: I realise it's common to use log response ratios when comparing large amounts of data, but why not directly use the percentage change to quantify drought effect size?

Response: the log response ratio is used to derive the test statistics following Lajeunesse (2011) and then back converted to percentage change.

L. 242-243: given the large variability in hydraulic behaviour observed within a genus, is it reasonable to use the genus average as a proxy here? And how many of the location points are affected by this assumption?

Response: yes, we agree that there can be large within genus variability in wood density and hydraulic behaviour. However, across neotropical tree species about 74% of the variation in wood density can be explained by genus level variability (Chave et al., 2006), so genus level wood density could be regarded a useful proxy. Genus averaged wood density was used in 127 cases out of a total of 834 individuals measured. As the wood density was averaged per study, we believe that the effect of using genus averaged wood density instead of species averaged wood density is small. The alternative would be to not provide a wood density value to this individual, which would probably cause more bias in the study averaged wood density than providing the genus average. We have now included these considerations and the number of species where we used the genus average in the revised paragraph.

L. 254: the reference to Figure 2a is needed here too

Response: the reference has been included in the revised version.

L. 260: I find hard to believe that this is an actual result and not simply a product of the methods used to calculate the leaf-level transpiration....

Response: the result that on average leaf transpiration does not change from the wet to the dry season (see also final major comment and figures), follows from the averaging of study level responses of 25 studies from which 11 studies showed a (marginal) increase in leaf-level transpiration and 14 studies a (marginal) decrease in leaf-level transpiration from the wet to the dry season (Figure 5 b). Furthermore, the same result is found when looking at tree scale transpiration which is independent from our calculation of VPD and leaf transpiration. The bias towards studies measuring low wood density trees in sun-exposes canopy positions likely contributes to the overestimation of the dry season decline in stomatal conductance and therefore leaf transpiration (this bias is discussed in the Discussion).

L. 265: but a drop in Ψl *is observed!*

Response: yes, this is confusing and has now been reformulated.

L. 275-276: the authors could mention that this is in line with the findings of Rosas et al. 2019 along a mesic-xeric gradient (although their study is not on neotropical species)

Response: we don't see how this sentence about alternating stem and canopy growth relates to the work of Rosas et al. 2019, maybe we have the incorrect paper? We read: "Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient" in New Phytologist.

L. 304 (and later): the "WUEi" notation is inconsistent with the "iWUE" notation used in the introduction

Response: this has been changed to iWUE in the revised version of the manuscript.

L. 311: "we observe that" is not needed

Response: agree, this has been omitted.

L. 315: typo: "marginal" should be "marginally"

Response: this has been corrected.

L. 322: give the ranges of variation?

Response: this sentence is confusing and has been omitted in the revised version.

L. 320-328: the findings would benefit from being broken down in terms of the dry season (significant) vs episodic drought (mainly not significant)

Response: agree, only for stomatal conductance and leaf transpiration is the relationship with wood density significant ($p < 0.05$) during episodic drought and shows a similar relationship as during seasonal drought. We have restructured and reformulated this paragraph.

L. 334: the authors need to state that the relationship is not significant...

Response: yes, we have added this in the revised version of the manuscript.

L. 336: "intermediate response" is very vague, please reformulate

Response: "intermediate response" will be omitted, "midday ψl declining parallel to a decline in pre-dawn ψl"should be a sufficient description of the midday leaf water potential response to declining pre-dawn leaf water potential in the intermediate wood density group. This has been reformulated.

L. 337-342: these findings are very useful!

Response: thank you.

L. 344-346: How is it "similar"? Fig. 6a seems to show far less significance and way more scatter than Fig. 5b

Response: we agree that this sentence is vaguely formulated. By "similar" we refer to the similarity in the relationships between wood density and the direction and magnitude of leaf and tree scale transpiration. Both show an increase of transpiration from the wet to the dry season in studies that measured high wood density species and a decline of transpiration in studies that measured low wood density species. This sentence has been reformulated to highlight what we mean by similar.

L. 356: why "hydrological"? Do the authors mean hydraulic?

Response: yes, we changed this to hydraulic.

L. 358: please replace "cancelled out" by "offset"

Response: this has been changed.

L. 392-394: I don't follow this sentence.... these effects can be consistently observed for weeks, and even months? Do the authors mean that leaf effects are typically observed on shorter time scales due to the "life expectancy" of a leaf compared to a tree, or to an ecosystem?

Response: yes, this is partly what is referred to here but not explicitly mentioned. Leaf shedding and flushing can be a mechanism that results in leaf scale responses being visible on shorter time scales but on even shorter timescales also the opening and closure of the stomates. The purpose of these two sentences is to highlight the presence of buffering in the system, in this case because of non-structural carbohydrates, that could result in the observed inconsistencies in drought responses going from the leaf to the ecosystem. This sentence has been reformulated.

L.405-406: the mention of these "ENSO swings" would be a better fit L. 400, right after the list of references. But what is an ENSO swing? This is never defined...

Response: this sentences has been moved and reformulated.

L. 398-407: I'm not entirely clear why the increase in the frequency of episodic droughts is not first mentioned in the results section?

Response: this is increase in episodic drought frequency is now elaborately mentioned in the results (3.2, first paragraph)

L. 538-540: this should come earlier, after L. 120-123

Response: these sentences have been removed following suggestion of referee #2

L. 546: but can also be explained by plant capacitance

Response: we would like to highlight the importance of deep roots to survive long droughts here. We discuss the importance of plant capacitance in other paragraphs of the Discussion.

L. 564: typo: missing "and" after "environments"

Response: "and" has been included.

Response to Referee #2

In this study, Janssen et al perform a meta-analysis to look to drought impacts on carbon and water exchange across scales ranging from leaf, to plant, to ecosystem in neotropical rainforests. In particular, the authors contrast physiological responses from seasonal water stress versus 'episodic' drought events. In doing this, the authors also look at wood density as a proxy for plant physiological responses. Its clear that the authors put in a significant amount of work through compiling 138 studies across 229 sites and this study will clearly contribute to the physiological literature on forest drought responses. I do have some major revision suggestions before publication which are summarized here and, in some cases, elaborated in the line specific comments below.

Response: thank you for your elaborate review of our manuscript and acknowledging the work that was put into creating the database behind the meta-analysis. We believe that your comments and suggestions have greatly enhanced the quality of the manuscript. Below we will respond to the major and minor comments raised by you in your report and describe where we made changes in the manuscript following your comments and suggestions.

1) I think that the manuscript would benefit from reframing of the dry season 'drought' as a routine period of decreased water availability. When I think of droughts, I think of a prolonged period of abnormally low rainfall. Given that dry seasons occur every year, I don't see them meeting this definition. This reframing would provide a nice platform to discuss physiological responses to routine (seasonal) stress, such as phenology, versus episodic stress and can help get at important physiological mechanisms. This would involve some substantial reworking of the text, but I think it would really help the story line.

Response: we agree that seasonal drought would not meet the criterium of being a prolonged period of abnormally low rainfall and we highlight this distinction with episodic drought and multi-year drought in the Introduction (L50-L54). However, the term "seasonal drought" is widely used in the literature (Esquivel-Muelbert et al., 2017; Rowland et al., 2013; Stahl et al., 2013) and leaf, tree and ecosystem processes similar to episodic drought are operating during seasonal drought. We discuss the differences between seasonal and episodic drought in the Discussion section 4.3 and mention how for example phenology is likely driving the observed seasonal responses in leaf flushing, shedding and stem growth.

2) Some of the methods are confusing and I think elaborating a bit more, providing and providing a table might help. See line specific comments below

Response: referee #1 also provided suggestions to improve the readability of the Methods. Changes in the text have now been made to elaborate on the Methods, including the calculation of VPD (section 2.1), leaf and tree transpiration (section 2.2) and dry season and drought definition (section 2.3). The requested table with database diagnostics has now been added to the supplement (Table S1).

3) The Figure legends need to be more descriptive of all the features in the figures

Response: the Figure captions and legends have been improved in the new versions of the Figures. See specific comments on the Figures about the exact changes in each Figure.

4) Overall the manuscript does an impressive job discussing a range of processes, but the reader might be more attentive if it were a little shorter. Where possible, I would suggest the authors *minimize extraneous discussion. In particular, I think talking about isohydricity requires significant motivation for a general audience (which is not provided), so I would cut this text.*

Response: thank you. We agree that the readability of the paper would improve if it were shorter. While preparing the revised version we have critically examined every paragraph to reduce the length of the manuscript. In the revised version of the manuscript we do not longer use the concept of isohydric and non-isohydric behaviour because, as you mention, it is not suitable for the broad audience of Biogeoscieces (specific comment L121). Furthermore, we agree that focusing on the mechanisms is more interesting that focusing on the (debated) concept of isohydric vs non-isohydric behaviour. Omitting the isohydric vs non-isohydric text has significantly reduced the length of the introduction.

Line-specific comments:

L21-22 There is nothing to back up this statement on LSMs. I suggest the authors remove it

Response: See also specific comment of referee #1. The statement has been rephrased to: ""We present new insights into the functioning of tropical forest in response to drought and present novel relationships between wood density and drought responses that can help guide the parametrization of land surface models."

L35 Khanna et al 2017 Regional dry-season climate changes due to three decades of Amazonian deforestation

Response: thank you for the literature suggestion, Khanna et al. 2017 has been added in the revised version of the manuscript.

L50 after going through the MS, I am confused about where the multi-year drought is presented in the authors analysis

Response: no it is not presented, see for the justification of omitting multi-year droughts L70-71

L53-54 This is exactly why I would argue that 'seasonal drought' is a misnomer

Response: see response to major comment #1.

L121 The concept of isohydricity/anisohydricity will likely not be familiar to a broad audience at Biogeosciences. I would encourage the authors to eliminate the jargon and focus on the mechanisms of interest (see Martinez-Vilalta 2016 "Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept") or else devote more space to describing isohydric behaviour

Response: this paragraph has been removed in the revised version of the manuscript, following your suggestion. See also major comment #4.

L131-132 But the authors actually try and demonstrate that wood density is usable as a proxy first, so isn't this more of a hypothesis?

Response: we agree this was a confusing sentence. We have restructured this paragraph.

L145 where does the multiyear drought aspect come in that the authors mentioned in the intro? Intro overall: The introduction is on the longer side (as is the manuscript) and the three separate sections do not have a smooth transition. I would try to combine 1.2 and 1.3 and streamline the text. Given that sections 1.2-1.3 are more about the mechanisms, I would put thes sections first and then say that different types of physiological stress also impact C and W fluxes including seasonal, routine decreases in water availability versus droughts

Response: thank you for your suggestions on restructuring the Introduction. We have now omitted explaining the concept of isohydric vs non-isohydric behaviour from the Introduction, making it significantly shorter. We would like to keep the structure of the three subsections in the Introduction as this structure mirrors that of the results and somewhat also the discussion: 1) what types of drought are there? 2) what are the average responses observed? and 3) can wood density/hydraulic behaviour explain differences between studies? We think this is a logical structure of the Introduction but we agree that many different structures are possible because of the many dimensions present in the meta-analysis (types of drought, different scales: leaf, tree, ecosystem) that have always presented a challenge on how to structure the text.

L152 ERA5 citation?

Response: a citation to the ECMWF website is now included.

L153-155 It would be good for the authors to say how many studies were associated with each of these diagnostics and how many studies had multiple observations, maybe a table would be useful?

Response: we have now added a table with a summary of the database in the Supplement of the revised version of the manuscript (Table S1).

L157-159 I am confused about how observations were calculated/recorded across scales? Could the authors elaborate? For example, were ecosystem-level measurements independent from leaf level, or were different levels calculated using observations from different scales by the authors? Both more details and a table detailing number of measurements for each diagnostic and number of studies that cover multiple diagnostics and scales would help

Response: the scales refer to the native "resolution" on which measurements were provided in the source papers. Many studies that measured leaf an tree scale responses provided data on the individual tree level, giving also a species and genus name. For these studies we could link these individual observations to a wood density value. However, many studies reporting ecosystem level responses provided data on the ecosystem level, e.g. 1 ha of forest. We have now included an extensive table in the Supplement (Table S2) which details which measurements were retrieved from each study and each site in the database, specified on the scale of the measurement (leaf, tree or ecosystem). We hope that this table will provide an overview for the reader who is interested on exactly what every study in the database measured and how we subdivided these measures into the three scales.

L161-162, this doesn't need to be included

Response: agree, this is omitted. See also specific comment by referee #1.

L166-167 This is a huge amount of work, I commend the authors

Response: thank you.

L170 it would be good to say the spatial resolution and include a citation for on ERA5 (30km?)

Response: yes indeed, 0.25 degrees is 27.75 km at the equator. This information is now added in the revised version.

L171 monthly average midday VPD?

Response: yes, this is the monthly averaged VPD at midday (12:00). We have now more elaborately described how we derived monthly averaged VPD at midday in the Methods.

L187 how was this error estimated?

Response: this was estimated as the RMSE (3.25 kg dm^{-2} d^{-1}) divided by the mean daily transpiration rate (9.56 kg dm^{-2} d^{-1}) = 0.34 = 34%. We have now omitted this confusing sentence and included an equation (new equation 3) to clarify how we estimate total daily transpiration.

L219 Figures should be renumbered so Fig 2 comes after Fig 1

Response: this reference to Figure 4 was not necessary and has been omitted in the revised version of the manuscript.

L208-209 It would be good to include a possible caveat about uncertainty associates with ERA5 soil moisture (which I presume is modeled)

Response: we have now compared ERA5 derived REW (based on soil moisture) with site measured soil water potential (Supplement Figure S2) and included a sentence that links to this Figure. In the new sentence we also refer to the possible uncertainties in the ERA5 soil moisture and explicitly mention that ERA5 data is a product of data assimilation and modelling.

L212-213 why the 65% and 10% quantiles? Did the authors test the sensitivity of their results to this assumption?

Response: the lack of a "sensitivity analysis" was also noted by referee #2 L212-213. In the revised version of the manuscript we have now included as sensitivity analysis (see Methods) and we included the results of this sensitivity analysis in the results (referring to new Figure S8 and S9), and discuss its implications in the Discussion.

L220 Could a study be both a dry season and episodic drought? I am a little confused about the partitioning. Also, where does multi-year drought come in?

Response: the partitioning is mentioned in the Methods section 2.3 "Dry season and drought definition", 10% of the driest dry season months were classified as episodic drought (and not anymore as dry season). We simplified the wet season / dry season definition in the revised version of the manuscript, using only the 10% quantile threshold and not the 65% threshold to delineate between wet, dry and episodic drought months. We hope this has helped to make the Methods in general more clear to the reader.

L225 did the authors check to see if it was necessary to log the response? Where did the ENSO data come from?

Response: the log-response ratio was calculated because this is the standard in the method used: the log transformed ratio of means (Lajeunesse, 2011). The ENSO data was retrieved from NOAA, a reference to this dataset has now been included in the revised version.

L254 how can predawn wp be positive 0.22?! Please check for a typo

Response: the minus sign unfortunately ended up on the previous page.

L281 Could the authors include Reco in some of the figures, they refer a change in Reco several times in the text but no visuals are provided

Response: Reco is the same as Ecosystem respiration in Figure 3 and 4. We have removed this abbreviation altogether.

L363 typo include 'us'

Response: yes, this is a typo. This has been corrected.

L370 denoted iWUE previously

Response: yes, this has been corrected.

L401 it is also true that there are more observations post 2000. The authors should discuss how this might impact their results

Response: to avoid a sampling bias, we have now also counted the number of episodic drought months in a regular grid across the entire study area (new Figure S3) and describe this in the Methods (2.3 2nd paragraph), Results (3.2 1st paragraph) and Discussion (4.2 1st paragraph).

L419 it would be nice to put these numbers in a physiological context

Response: it is not entirely clear what is meant by this comment. Could you clarify?

L451-458 I think there is a really nice opportunity to contrast tree physiological strategies when exposed to routine stress (the dry season) versus drought that the current narrative doesn't allow for when both are classified as drought

Response: We agree that this comparison is important and, although we prefer sticking to the term seasonal drought (see further), comparing seasonal drought (routine stress) to episodic drought is one of the main objectives of the meta-analysis. There are basically two reasons why we use the term seasonal drought: 1) the term "seasonal drought" is commonly used in the literature and 2) the difference in drought conditions between the wet season and dry season is comparable to the difference between a regular dry season and episodic drought (Figure 2).

L461 is it the short timescale, or that fact that the plants are used to this type of stress and use phenology to deal with it?

Response: it is not clear what is driving these tree scale responses to drought and on which time scale these responses operate (Doughty et al., 2015; Hofhansl et al., 2014). The purpose of this sentence was to give a potential explanation for the lack of leaf litterfall and leaf flushing responses during episodic drought. We argue that this could be the result of the phenology time-scales and the amplitude of leaf exchange overwriting the more subtle responses to drought, if there are any.

L464 Or maybe title: how do we scale from the leaf to the ecosystem? This is a universal problem in ecology that researchers across many subdisciplines will sympathize with

Response: thank you for the nice suggestion. We have now used the suggested title in the revised manuscript.

L502 see previous suggestion about isohydricity

Response: noted. All mentions of isohydric/non-isohydric behaviour have been omitted in the revised version.

L536 This isn't a great comparison. The authors of this manuscript analyze site-specific data whereas the spatial scale of the Konings study is o(100km). For me, this paragraph does not contribute much to the study and in general I think the isohydricity framework is not useful here (and otherwise)

Response: we agree this is not a great comparison, these two sentences are now omitted.

L575 LSMs are brought up in only in the abstract and conclusion. It doesn't add to the discussion and I would remove this

Response: noted, we do not mention LSMs anymore in the Conclusions in the revised version.

L582 How should they be used to benchmark LSMs? If the authors insist on including this, please the need to spell out the methodology rather than throwing it in as a concluding sentence Other relevant citation: Detto 2018 "Resource acquisition and reproductive strategies of tropical forest in response to the El Niño-Southern Oscillation"

Response: the reference to LSMs are removed.

Figures combined comments

Figure 1

Fig. 1 panel a make lat/lon bigger

Response: the latitude, longitude axes ticks are now larger.

b) its really hard for me to wrap my head around what the authors mean by this metric, can they elaborate?

Response: an explanation of the calculation of the number of episodic drought months per year is now provided in the figure caption.

d) What do the dots mean? Please describe this in the legend and also detail what dark and light gray correspond to legend

Response: the explanation of the dot colour and the dark and light grey lines are now explained in the figure caption.

(e) it would be good to remind the reader what the positive/negative ENSO index means

Response: the meaning of the positive and negative ENSO index is now included in the figure caption.

L1131 "terrestrial" isn't capitalized

Response: noted, this has now been changed.

Fig. 1a: the K34 site should be indicated on the map given Fig. 1d and 1e

Response: the location of K34 is now indicated in yellow on the map in the revised version.

Fig. 1b: this is averaged across sites, right? I wonder whether it would make more sense to actually average the episodic drought months across the whole area of neotropical forests shown on the map. This would potentially reduce sampling biases in concluding that episodic droughts have been *increasing in neotropical forests. Alternatively, the authors could consider weighting this by the number of monthly observations per year.*

Response: yes, this is averaged across sites. The number of episodic drought months counted in Fig. 1b are independent of the monthly observations retrieved from the literature as all months classified as episodic drought in the time series (1979-2019) at that each site are included. We have now also calculated the number of episodic drought months across the neotropics in a regular grid of 1° (Figure S4) to compare this to the counted number of episodic droughts in Fig. 1b. The data shows a similar increase in episodic drought months per year over the 1979-2019 timespan. We discuss these findings and refer to Figure S4 in the results (Lxx) and discussion (Lxx).

Fig. 1e: visually, it would be very nice if the ENSO index was coloured to match the wet and dry season and the episodic droughts

Response: thank you for the suggestion. Wet and dry season colouring of the ENSO index is not possible as wet and dry season occur at different times across the study area. However, we now coloured the ENSO index based on the counted number of episodic droughts across the sites per month to show at which ENSO modes episodic droughts occurred in the study area.

Figure 2

Fig. 2a: where do the top soil Ψs data come from? The caption says published data, but I didn't find it in the methods?

Response: the references for the soil matric potential are in the supplementary material (main database excel file). We now refer to the supplementary database in the figure caption and included a sentence about the soil matric potential in the methods section on data collection.

Fig. 2a and 2b: yes to the mention of capital letters in the legend, but what does it mean when letters are coupled (e.g. AB in the dry season in Fig. 2a) or when the letter A or B appear during episodic droughts?

Response: for Fig 2a this indicates that there is a significant difference in topsoil water potential between the wet season (A) and episodic drought (B) but not between the dry season and either the wet season or episodic drought (AB). We now explain the coupling of capital letters in the final sentence of the figure caption.

Fig.2: I imagine the horizontal lines in the box plots show the median, the boxes themselved interquartile ranges, the vertical lines the 5th-95th percentiles and the points are outliers? This needs to be mentioned in the legend

Response: yes exactly. The values depicted in the boxplots (median, interquartile range, min/max and outliers) are now provided in the figure caption.

Fig. 2 can the authors denote the sample size above each category in the figure? For example, does n=3 for Episodic drought soil-leaf hydraulic conductance in panel b? Make sure to describe the figure fully (detail quantile boxes, median line, error bars, and outliers) in the legend

Response: the sample size is now denoted above Figure 2 a and b. Other descriptions have also been included in the figure caption (see previous comments on this figure).

Figure 3, 4

Figs. 3 4: what do the horizontal lines represent? Ranges?

Response: the horizontal lines are the 95% confidence interval range, this description has now been included in the figure caption.

Additionally, it would be useful:

1. *to also mention the number of data points (or average number of data points per study/site) in brackets;*
2. *to visually separate the variables that were directly retrieved from the literature from those that necessitated further calculations.*

Response: we have combined Figure 3 and 4 after the suggestion by referee #2, making the visual comparison of seasonal and episodic drought responses easier. However, this makes the new Figure 3 also more crowded with symbols and numbers. We therefore would not like to add more descriptive statistics besides the number of individuals studies and sites for each measure during each drought comparison. The number of data points can be retrieved from the new Supplementary Table S1. Furthermore, separating the variables that are directly retrieved from the literature and those that required further calculation would add another dimension to this already crowded figure. Besides, some of the variables have data points directly from the literature as well as recalculated values (for example daily transpiration) and some variables are calculated but are a simple difference between two variables directly retrieved from the literature (for example the water potential gradient).

Fig. 3-4 I would combine these two figures into 1 2-column 3-row figure. I generally really like this format and found it very effective in the Ainsworth review. Great job describing all aspects of the figure in the legend

Response: thank you. We have now combined Figure 3 and 4 into a single figure (new Figure 3) following your suggestion. We hope this new Figure 3 will benefit the comparison of seasonal and episodic drought responses in the revised version of the manuscript.

Figure 5, 6

Figs. 5 6: so bigger points mean smaller errors? Does that also play a role in the weighting of the solid and dashed lines?

Response: yes, the size of the points is determined based on the inverse of the sampling variance of that particular study (i.e. precision) and yes, the model is also constructed using inverse-variance weights. These details have now been added to the Methods and are described in the caption of the revised figure.

Fig 5-6 I would combine these figures into a 2-c 3-r figure

Response: Figure 5 and 6 have now been merged following your suggestion, This is now the new Figure 4.

The point size is the inverse of the sample standard error of the effect size in the study.–> so studies with a smaller SE have a larger dot? Moderator= independent variable?

Response: this is now explained in the Methods and the caption of the new Figure 4. See also the response to the final comment of referee #1.

Fig 5 legend, make sure to walk the reader though each panel

Response: the caption has now been adapted to guide the reader through each panel of the Figure.

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Drought resistance increases from the individual to the ecosystem level in highly diverse neotropical rain forest: a meta-analysis of leaf, tree and ecosystem responses to drought

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Abstract. The effects of future warming and drying on tropical forest functioning remain largely unresolved. Here, we conduct a meta-analysis of observed drought responses in neotropical humid forests, focused on carbon and water exchange. Measures of leaf, tree and ecosystem scale performance were retrieved from ~~138~~ 145 published studies conducted across ~~229~~ 232 sites in neotropical forests. Differentiating between seasonal and episodic drought we find that; (1) during seasonal drought, the increase of atmospheric evaporative demand and a decrease of soil water potential results in a decline of leaf water potential, stomatal conductance, leaf photosynthesis and stem diameter growth while leaf litterfall and leaf flushing increase. (2) During episodic drought, we observe a further decline of stomatal conductance, photosynthesis, stem growth and, in contrast to seasonal drought, also a decline of transpiration. Responses of ecosystem scale processes, productivity and evapotranspiration, are of a smaller magnitude and often not significant. Furthermore, we find that the magnitude and direction of a drought-induced change in photosynthesis, stomatal conductance and transpiration reported in a study is correlated to study-averaged wood density. Although wood density is often not functionally related to plant hydraulic properties, we find that ~~Therefore, wood density~~ it is a good proxy of hydraulic behaviour and can be used to predict leaf and tree scale responses to drought. We present new insights into the functioning of tropical forest in response to drought and present novel relationships between wood density and plant drought responses that can help guide the parametrization of land surface models~~We present new insights into the functioning of tropical forest in response to drought and offer a response-benchmark for land surface models~~.

1 Introduction

The neotropical rainforests of South and Central America, with the Amazon Basin at its centre, cover the largest tract of tropical forest on Earth. As such, these forests are a crucial component of the regional and global climate system as a source of convective heat and moisture, driving atmospheric moisture transport and precipitation patterns (Poveda and Salazar, 2004; Zemp et al., 2014). General circulation models project that South and Central America will warm by 2 °C to 5 °C in the coming decades under the business as usual emission scenario (Marengo et al., 2010). Furthermore, seasonal drought is expected to become more severe (Boisier et al., 2015; Malhi et al., 2009; Marengo et al., 2010). Undisturbed old growth forest in the Amazon Basin has increased in aboveground biomass since the 1980's, acting as a substantial sink of atmospheric carbon (Feldpausch et al., 2016; Phillips et al., 2009). However, recent drought events appear to have at least temporarily reversed the Amazon carbon sink through reduced productivity (Gatti et al., 2014; Yang et al., 2018b), elevated tree mortality (Feldpausch et al., 2016; Phillips et al., 2009) and increased emissions from fire (Aragão et al., 2018; Van Der Laan-Luijkx et al., 2015; Van Der Werf et al., 2008). Furthermore, the integrity of neotropical forest~~s~~ may be threatened by unforeseen feedback mechanisms triggered by drought and deforestation (Khanna et al., 2017; Zemp et al., 2017). These vegetation-atmosphere feedbacks can reduce atmospheric moisture recycling and increase carbon emissions, which further amplifies forest loss and global climate change (Cox et al., 2000, 2004; Davidson et al., 2012; Erfanian et al., 2017; Exbrayat et al., 2017; Malhi et al., 2009).

Despite the critical role of neotropical forests in driving future climate scenarios, there are large uncertainties surrounding the sensitivity of these forests to drought. Uncertainties are partly the result of the biological diversity found in neotropical forests as the magnitude and direction of a response to drought is found to be strongly dependent on the species measured (Bonal et al., 2000a; Domingues et al., 2014). Also, uncertainties arise as droughts differ in length, periodicity and severity (Bonal et al., 2016; Marengo et al., 2011; Meir et al., 2018). Finally, ecophysiological responses to drought occur on a multitude of spatial and temporal scales. These responses range from the almost instant closure of the stomata on a single leaf, to large scale tree mortality that has persistent effects on many ecosystem processes (Brando et al., 2008; Rowland et al., 2015b, 2015a). Currently, there is no quantitative overview or understanding of how neotropical forests respond to different intensities of drought, from the leaf level up to the entire ecosystem. Below we formulate three key issues that guide our meta-analysis.

1.1 What type of droughts occur in neotropical forests?

Here, we differentiate three types of drought that differ in periodicity and severity: seasonal drought, episodic drought and multi-year drought. Seasonality in precipitation is widespread in neotropical forests. Tropical humid forests loose roughly 100 mm of water every month through evapotranspiration (da Rocha et al., 2004; Shuttleworth, 1988). Months receiving less than 100 mm of rainfall will thus result in a precipitation deficit, these months are generally referred to as dry season months (Aragão et al., 2007; Sombroek, 2001). Seasonal droughts are by definition periodic and trees are generally found to be adapted to such a seasonal decline in precipitation (Brando et al., 2010; Goulden et al., 2004; Hutyra et al., 2007).

Episodic droughts, on the other hand, are caused by anomalous climatic conditions, primarily those imposed by strong El Niñ~~n~~o Southern Oscillations (ENSO) and tropical North Atlantic sea surface temperature anomalies (Marengo et al., 2011). Episodic droughts often coincide with record breaking air temperatures in the neotropics ~~and high vapour pressure deficits~~ (Jiménez-Muñoz et al., 2016; Lee et al., 2013; Panisset et al., 2017). Elevated air temperature can directly impact plant functioning through physiological heat stress (Doughty, 2011; Doughty and Goulden, 2009a) but it also drives a non-linear increase of atmospheric vapour pressure deficit (VPD). ~~and~~This increase of evaporative demand during drought can amplify drought conditions through increased evapotranspiration, accelerating soil drying (Jung et al., 2010) and increasing the risk of hydraulic failure (Mcdowell et al., 2008)~~ and heat stress~~. The amplification of plant drought stress during episodic drought through the interaction of soil drying, high air temperatures and evaporative demand ~~, resulting in so-called~~have been termed "~~global-change type~~hotter droughts" (Allen et al., 2015; Breshears et al., 2013) and are expected to become more frequent and sever with climate warming.

Multi-year droughts are defined as a more permanent reduction of precipitation spanning years to decades. ~~, as projected by some climate model simulations (Boisier et al., 2015; Malhi et al., 2009).~~ Long term records of river discharge and oxygen isotopes in tree rings indicate that neotropical forests experienced several multi-year droughts in the 20th century, notably in the 1960s (Brienen et al., 2012; Marengo et al., 2011; Richey et al., 1989). To date, the effect of prolonged rainfall reduction on leaf, tree and ecosystem functioning have only experimentally been assessed in two throughfall exclusion experiments at Tapajós and Caxiuanã in the eastern Amazon (Fisher et al., 2006; Meir et al., 2009; Nepstad, 2002). The results from the Tapajós and Caxiuanã experiments have been previously synthesised (e.g. Meir *et al.*, 2009, 2018; da Costa *et al.*, 2010a) and much of our knowledge about leaf, tree and ecosystem scale responses to multi-year droughts in tropical forests originates from these experiments. Therefore, and because of the low number of replicates (i.e., 2) of such experiments, this meta-analysis will focus only on the effects of seasonal and episodic drought on leaf, tree and ecosystem functioning.

1.2 How is drought impacting leaf, tree and ecosystem scale processes?

On the leaf scale, seasonal and episodic drought are often found to result in a downregulation of stomatal conductance; the ease by which CO_2 and water vapor can diffuse between the atmosphere and the leaf intercellular spaces through the stomates (Hogan et al., 1995; Huc et al., 1994). The most recent evidence suggests that stomates progressively close in response to a decline in leaf water potential (ψ_l) (Buckley, 2019; Choat et al., 2018; Drake et al., 2017; Martin-StPaul et al., 2017). Here, we focus specifically on how drought-induced changes in ψ_l, the water potential gradient and the different conductance's along the hydraulic pathway are driving the observed drought-induced changes in productivity and transpiration. During steady state transpiration, ~~leaf~~ transpiration is given by:

$$E = k_{sl}(\psi_s - \psi_l) = G_c \times VPD \qquad (1)$$

where E is the ~~leaf~~ transpiration rate, k_{sl} the soil to leaf hydraulic conductance~~, and~~ ψ_s is the soil water potential in the root-zone, G_c is the crown conductance and VPD_s is the leaf-to-air vapor pressure deficit. The first part of equation 1 describes the liquid phase water transport from the root to the leaf through the xylem, while the second part describes the vapor phase transport of water from the leaf to the atmosphere through the leaf stomates. During drought, k_{sl} declines sharply as a result of reduced hydraulic conductance of drier soil as well as reduced hydraulic conductance of the xylem as a result of xylem embolism (Fisher et al., 2006). It follows that, all things being equal, the decline of k_{sl} should be balanced by a decline of G_c

that is achieved by progressive stomatal closure (Meinzer et al., 1995). ~~Rewriting equation~~ Nonetheless, equation 1 also shows that transpiration can stay the same, increase or decrease during drought, depending on if a decline in k_{sl} and G_c is compensated for by an increase of the water potential gradient ($\psi_s - \psi_l$) or atmospheric evaporative demand (VPD) .~~as:~~

~~$\psi_l = \psi_s - \frac{E}{k_{sl}}$ (2)~~

~~shows that a drought-induced decline of ψ_l can be a compound result of a decline in soil water potential, a reduction of soil to leaf hydraulic conductance and increased leaf transpiration.~~

Progressive ~~S~~stomatal ~~downregulation~~ closure does not only constrain ~~potential~~ transpiration from the leaf but also the diffusion of CO_2 into the leaf, ~~potentially~~ limiting leaf photosynthesis. In neotropical humid forests, ~~T~~the ~~decline of~~ stomatal conductance ~~in~~ response to drought is ~~often~~ generally larger compared to the decline in leaf photosynthesis, resulting in an increase of intrinsic water use efficiency (iWUE) (Bonal et al., 2000a; Santos et al., 2018). It is unclear how leaf-scale processes respond to drought in neotropical humid forest, with some studies reporting strong reductions in stomatal conductance, leaf transpiration and photosynthesis during seasonal and episodic drought (e.g. Hogan et al., 1995a; Huc et al., 1994; Sendall et al., 2009; Wolfe et al., 2016) while others report no significant change in stomatal conductance and photosynthesis and even an increase of leaf transpiration (e.g. Allen and Pearcy, 2000; Domingues et al., 2014; Fisher et al., 2006).

Leaf scale responses to drought can propagate to the tree scale, with reduced growth of the stem and new leaves, increased leaf shedding and litter fall and reduced tree daily transpiration (Brum et al., 2018; Doughty et al., 2015; Fontes et al., 2018; Hofhansl et al., 2014; Phillips et al., 2009). Furthermore, the combined drought response of all individual trees in the ecosystem contributes to the observed ecosystem scale response to drought. Reduced leaf photosynthesis and leaf and stem growth can result in a decline of gross ~~ecosystem~~ primary productivity (GP~~E~~P) and consequently a decline of ~~aboveground~~ net primary productivity (~~A~~NPP) while reduced tree transpiration might result in a decline of ecosystem evapotranspiration. Moreover, increased leaf litterfall in response to drought can boost microbial respiration and result in an increase of ecosystem respiration ~~(R_{eco})~~ (Sayer et al., 2007). ~~For example,~~ However, soil respiration is limited by temperature and moisture in neotropical humid forests and is found to decline with a dry season decline in soil moisture (Chambers et al., 2004; Sotta et al., 2004; Zanchi et al., 2014). ~~Next to the vegetation response to drought, a drought response of the microbial community as a result of reductions in soil moisture, atmospheric moisture and increased temperatures can contribute to the ecosystem scale response to drought.~~ ~~For example, soil respiration is limited by temperature and moisture in neotropical humid forests and is found to decline with a dry season decline in soil moisture (Chambers et al., 2004; Sotta et al., 2004; Zanchi et al., 2014).~~ The integration and synthesis of the observed drought responses on the leaf, tree and ecosystem scale ~~these three key spatial scales~~ has not been carried out but can act as a method to identify critical drought response mechanisms and highlight current knowledge gaps.

1.3 Can hydraulic behaviour explain differences in drought responses among species and studies?

Different tree species show markedly different responses to drought, both on the leaf level (Bonal et al., 2000a; Domingues et al., 2014) and the individual tree level (Esquivel-Muelbert et al., 2017a, 2017b; Phillips et al., 2009). The magnitude and direction of observed drought~~-induced~~ responses depend on the hydraulic behaviour of the particular species measured in that study (Bonal et al., 2000a; Fisher et al., 2006; Machado and Tyree, 1994). For example, species can adopt different drought ~~avoiding and drought tolerating~~ avoidance and tolerance strategies (Volaire, 2018). Drought avoiding strategies aim to avoid a dangerous decline in ψ_l that could ~~initiate~~ lead to significant xylem embolism and thus damage the hydraulic pathway. Maintaining a stable high ψ_l during drought can be achieved by strict stomatal control on leaf transpiration (Huc et al., 1994; Machado and Tyree, 1994), increasing deep soil water uptake (Bonal et al., 2000b; Brum et al., 2019), maintaining a high plant internal water storage and conductance (Tyree et al., 2003; Wolfe, 2017) and through leaf shedding (Wolfe et al., 2016). Conversely, ~~the~~ drought tolerance~~t~~ strateg~~y~~ies imply~~ies~~ that low leaf and xylem water potentials are tolerated without significant and irreversible embolism-induced losses of hydraulic ~~conductance and leaf turgor~~function (Maréchaux et al., 2015; Markesteijn et al., 2011a; Tyree et al., 2003). ~~Related to the drought tolerant versus drought avoiding dichotomy is the concept of isohydric versus non-isohydric behavior, where isohydric species maintain a stable and high~~ ~~ψ_l~~ ~~in response to soil drying (drought avoiding) while non-isohydric species lower~~ ~~ψ_l~~ ~~in accordance with a decline in soil water potential (Martínez-Vilalta et al., 2014; Meinzer et al., 2016). It is unclear whether neotropical forest tree species are generally isohydric as suggested by remote sensing analysis (Konings and Gentine, 2017) or non-isohydric as has been generally observed in situ (Domingues et al., 2014; Rundel and Becker, 1987; Tobin et al., 1999).~~

Tree hydraulic behavior is strongly dependent on the characteristics of the xylem sapwood (Janssen et al., 2020; Markesteijn et al., 2011b, 2011a; Meinzer et al., 2008b, 2008a; Wolfe, 2017). ~~Drought tolerant s~~Species that do not avoid dehydration through stomatal closure ~~characterized by non-isohydric behavior~~ are generally found to have xylem that is highly resistant to embolism, thus making them drought tolerant (Skelton et al., 2015; Vogt, 2001). Conversely, drought avoiding species are able to buffer midday declines in xylem water potential by using water that is stored in the sapwood (i.e. capacitance) and by strong stomatal control on transpiration (Borchert, 1994; Machado and Tyree, 1994; Meinzer et al., 2008b). ~~In this meta-analysis, we will use wood density as a proxy of hydraulic behavior and examine whether differences in study-averaged wood density explain the variability in observed leaf and tree scale responses to drought between different studies.~~ In neotropical tree species, sapwood capacitance and conductivity decline while embolism resistance generally increases with increasing wood density (De Guzman et al., 2017; Janssen et al., 2020; Meinzer et al., 2008b; Santiago et al., 2018). This suggests that low wood density species can be considered drought avoiders while high wood density tree species are characterized as drought tolerant. Wood density is often not functionally related to the specific hydraulic properties (conductivity, capacitance and embolism resistance) that are driving hydraulic behavior (Janssen et al., 2020; Lachenbruch and Mcculloh, 2014). Nonetheless, wood density is an easily interpretable and widely available plant trait and therefore a useful proxy to compare different studies in which more specific hydraulic properties and traits were not measured. ~~In this meta-analysis,~~ Therefore, we will use wood density as a proxy of hydraulic behavior in this meta-analysis and examine whether differences in study-averaged wood density explain the variability in observed leaf and tree scale responses to drought between different studies.

~~Here, we present a meta-analysis of a new database of neotropical forest responses to seasonal and episodic drought on three key spatial scales: the leaf, tree and ecosystem scale. We focus specifically on impacts of drought on carbon and water interactions. The aim of this meta-analysis is to: 1) provide a benchmark of neotropical humid forests responses to seasonal and episodic drought and identify inconsistencies when going from the leaf to the ecosystem scale. 2) identify differences and similarities between episodic and seasonal drought responses. And 3) explore the relationships between study-averaged wood density and the magnitude and direction of leaf and tree scale responses to seasonal and episodic drought.~~

2 Methods

2.1 Data collection

The data collection focussed on published observations from the lowland humid forest of the neotropics, roughly between 20° South to 20° North (Figure 1, a). We searched the literature present in the Web of Science between 1979 and 2019. This time frame matches the ERA5 reanalysis climate data ~~time series~~(ECMWF, 2019) that ~~were~~ was used to obtain harmonized meta-data for the retrieved literature. Publications were archived in a database if ~~i~~they contained one of the following measures: stomatal conductance, leaf photosynthesis, leaf water potential, stem sap flux density, stem diameter increment, leaf flushing, leaf litterfall, ecosystem evapotranspiration, gross ~~ecosystem~~ primary productivity, net primary productivity, ecosystem respiration and net ecosystem productivity. For studies that reported at least one of these measures, the observed values were stored in a database containing the reported value, the location and the month and year in which the measurement took place. For leaf scale measurements, all data included in the database were originally measured at midday (around 12:00 local time), except for pre-dawn leaf water potential which is measured just before sunrise (around 06:00 local time). Site measured soil matric potential was also included in the database. If possible, the leaf and tree scale measures of individual trees including genus and species name were stored in the database. Otherwise, site averages were used. Observations of ecosystem scale processes always consisted of site averages.

~~Using the site latitude and longitude, we created spatial points of all the site locations (Figure 1, a). These points could then be used to extract spatial data using the routine *extract* in the R package *raster* (Hijmans et al., 2019).~~ For every ~~The~~ site in the database, the site biome was extracted from the *t*~~*T*~~*errestrial ecoregions of the world map* from the World Wildlife Fund (Olson et al., 2001). Sites that were not located in the “Tropical and subtropical moist broadleaf forest” biome were omitted from the meta-analysis. Furthermore, the site elevation was extracted from the ALOS global 30m digital surface model (Tadono et al., 2016), which was aggregated to 1 km resolution using Google Earth Engine. ~~*World digital elevation model ETOPO5* from the~~

~~European Environmental Agency (2019).~~ All sites that were located at elevations higher than 1000 m a.s.l were regarded montane environments and were as such omitted from the meta-analysis. The final database used for the meta-analysis included observed drought responses from ~~138~~ 145 published studies conducted across ~~229~~ 232 sites in neotropical humid forests (Table S1 and S2).

Monthly averaged values of soil water content, air temperature and dewpoint air temperature at 2 meter above the surface were retrieved from the ECMWF ERA5 reanalysis product at 0.25 degree horizontal resolution (~28 km) (ECMWF, 2019). Values were retrieved for all the sites ~~from the ECMWF ERA5 reanalysis product~~ from January 1979 to August 2019. Monthly averaged air temperature and dewpoint temperature at four hourly averages (15:00 – 18:00 UTC) were used to retrieve monthly averaged midday (12:00 local time) temperature and dewpoint temperature in the four time zones covering the study area. These values ~~12:00 p.m.~~ were used to calculate monthly averaged midday vapor pressure deficit (VPD) following Buck (1981). The ERA5 retrieved monthly averaged midday VPD corresponded well with the monthly averaged midday VPD that was measured at 9 meteorological towers across the study area (Figure S1). Monthly integrated soil moisture over the entire soil profile was calculated as the weighted average of soil moisture content in ~~the~~ all four soil layers (0 – 189 cm below the surface) provided in the ERA5 product. In neotropical humid forest, the bulk soil water is taken up from the first 1.3 meter of soil but this can extend up to 10-12 meters during drought (Brum et al., 2019; Davidson et al., 2011). ~~-~~Integrated soil moisture was ~~then~~ used to estimate relative extractable soil water (REW) which is shown to capture both wet-dry season oscillations as well as episodic droughts (Figure 1 d~~, see section 2.3~~).

2.2 Data pre-processing and deriving additional measures

From the collected leaf, tree and ecosystem ~~performance~~ measures we derived additional measures of transpiration, productivity and water use efficiency. On the leaf scale, we estimated potential midday leaf-area specific transpiration ~~was calculated~~ as:

$$E_{pot} = g_s \times VPD \qquad (2)$$

where g_s is the midday leaf-area specific stomatal conductance to water vapor and VPD ~~the product of midday stomatal conductance and~~ is the monthly averaged midday VPD derived from the ERA5 reanalysis data. In this estimation we use atmospheric VPD instead of leaf-to-air VPD at the leaf surface, which are often decoupled in large leaved trees and dense tropical forest canopies (Jarvis and Mcnaughton, 1986; De Kauwe et al., 2017; Meinzer et al., 1997). Using atmospheric VPD likely causes a gross overestimation of absolute leaf transpiration estimates and these estimates should never be used as a measure of actual leaf transpiration. However, this meta-analysis deals with relative changes, so that this overestimation should not have a major impact on the drought-induced percentage changes in potential leaf transpiration. Instantaneous intrinsic water use efficiency (iWUE) at midday was calculated directly from the published data as:

$$iWUE = \frac{A}{g_s} \qquad (3)$$

where A is the midday leaf-area specific photosynthesis. Finally, the instantaneous actual water use efficiency (WUE) at midday was estimated as:

$$WUE = \frac{A}{E_{pot}} \qquad (4)$$

~~and instantaneous actual water use efficiency (WUE) were calculated as the ratios between leaf-area specific photosynthetic rate and stomatal conductance or leaf transpiration at midday, respectively.~~

On the tree scale, in ~~13~~ 17 out of ~~28~~ 34 studies that reported sap flux density results, only the maximum midday sap flux density values were reported but not the ~~integrated~~ summed daily transpiration rates. For these studies, ~~the integrated~~summed daily transpiration was estimated as:

$$J_{daily} = 24\left(\frac{J_{max}}{a}\right) \qquad (5)$$

where J_{max} is the daily maximum sap flux density and a is a parameter fitted using a linear regression ~~from a significant linear relationship (RMSE = 3.25 kg dm⁻² day⁻¹)~~ between ~~daily~~ maximum sap flux density and daily transpiration (Figure S~~1~~2). ~~Errors introduced by this approach were estimated to be less than 34% of the integrated daily transpiration rates.~~ Furthermore, we calculated the instantaneous soil to leaf hydraulic conductance on a sapwood area basis following Love and Sperry (2018):

$$k_{sl} = \frac{J_{max}}{(\psi_{l\,pd} - \psi_{l\,md})}$$
(~~3~~6)

where ~~J_{max} is the daily maximum sap flux density,~~ $\psi_{l\,md}$ is the midday leaf water potential and $\psi_{l\,pd}$ is the pre-dawn leaf water potential. Pre-dawn ψ_l is measured before the onset of leaf transpiration and considered a proxy of ψ_s in the ~~rooting~~ root-zone (Equation 1).~~.~~ Therefore, the difference between midday ψ_l and pre-dawn ψ_l is regarded a proxy of the midday water potential gradient within the tree, from the root up to the canopy. ~~(see also Equation 1).~~Finally, we estimated midday crown conductance following Meinzer et al. (1997):

$$G_c = \frac{J_{max}P}{VPD} \qquad (7)$$

where P is atmospheric pressure (kPa) and VPD is the monthly averaged midday VPD derived from ERA5 data.

On the ecosystem scale, the ~~above-ground net ecosystem productivity (ANPP)~~ total net primary productivity (NPP) and above-ground NPP (ANPP) were~~as~~ calculated as the sum of ~~biomass allocated to~~ stem growth and ~~biomass allocated to~~ canopy growth, and for NPP also including root growth (sensu Doughty et al., 2015a; Hofhansl et al., 2014). Finally, the ecosystem water use efficiency was calculated as the ratio between gross ~~ecosystem~~ primary productivity (~~GEP~~GPP) and ecosystem evapotranspiration (sensu Yang et al., 2016).

2.3 Dry season and drought definition

As the dry season progresses, soil moisture content, relative extractable soil water (REW) and soil water potential decline as daily evapotranspiration surpasses precipitation (see e.g. Wright *et al.*, 1992; Nepstad, 2002). The occurrence of rain ~~during or~~ at the end of the dry season generally results in a rapid increase of soil water potential and a relief of plant water stress (Fontes et al., 2018; Roberts et al., 1990; Tobin et al., 1999). Therefore, we define ~~the~~ dry season months as months in which REW is reduced relative to the previous month (Figure 1 d). The REW is the amount of soil water available for plant uptake, which is often expressed as the volumetric soil moisture scaled between field capacity (REW = 1) and permanent wilting point (REW = 0). However, as there are insufficient measurements to construct reliable soil water retention curves across the study sites, we could not calculate REW. Instead, we estimated a pseudo REW as the normalized integrated soil moisture from ERA5, with 0 in the driest month and 1 in the wettest month of the entire timeseries (1979-2019) at that specific site (Figure 1, 2). To avoid a rapid oscillation of dry and wet season months over time due to small reductions or increases in REW, we labelled initially classified single dry season months in between two wet season months as wet season, and vice versa. We find that, despite the uncertainties in ERA5 soil moisture data due to the underlying data assimilation and modelling, the ERA5 derived REW is able to accurately capture the seasonality of site measured soil matric potential (R^2 = 0.5, $p < 0.001$, Figure S3).

~~Some months in the middle of the wet season with high REW showed small reductions in REW compared to the previous month. To exclude these months from the dry season, all months with REW higher than the 65% quantile of REW were labelled as wet season months despite a reduction in REW. Subsequently, d~~Dry season months where REW was lower than the 10% quantile of REW in all dry season months were labelled as episodic drought~~s~~ months (Figure 1 d). The 10% episodic drought threshold value was chosen as a reasonably strict episodic drought definition while still yielding a large enough sample size for the statistical analysis to differentiate between episodic drought and a regular dry season. We also performed a sensitivity analysis for this drought threshold by shifting the threshold to 15% of the driest dry season months (wide definition) and to 5% of the driest dry season months (narrow definition). We counted per year the number of episodic drought months occurring at each site (Figure 1d) and in a regular 1° grid across the study area (Figure S4) to see how the occurrence of episodic droughts have changed over the past decades. We also used linear regression models to investigate correlations between ERA5 derived midday air temperature, midday VPD and number of episodic drought months per year (Table S3). ~~In three studies, additional months that were not initially classified as episodic droughts but were considered exceptional dry months in that study were classified as episodic drought months. These months were September 2002 at Tapajós in Domingues et al. (2014), April 1977 at Barro Colorado Island in Fetcher (1979) and January, February and March 2009 in Hofhansl et al. (2014).~~ The subdivision resulted in 2917 monthly observations in the wet season, 2917 in the dry season and 497 during episodic drought. That we end up with a significantly higher amount of episodic drought months in our meta-analysis than should be expected from the 10% quantile episodic drought threshold (i.e. 291.7) can be explained by a high number of samples in recent studies that covered the 2015 ENSO drought (Doughty et al., 2017; Fontes et al., 2018; Maréchaux et al., 2018; Rifai et al., 2018; Santos et al., 2018). Stem growth data from the extensive forest inventory dataset of Brienen et al. (2015) was also included in the database. Because these data ~~In studies where the measurement period~~ cover~~ed~~ multiple months, we labelled ~~time~~ census intervals that included at least three months of episodic drought as episodic drought and otherwise as dry season months for comparison ~~(Figure 4)~~. ~~The subdivision resulted in 3326 observations in the wet season, 3006 in the dry season and 624 during episodic drought.~~ Monthly values of the multivariate ENSO index for the period 1979-2019 were retrieved from the National Oceanic and Atmospheric Administration (http://www.esrl.noaa.gov/psd/enso/mei/). Strong ENSO years (1996-1997, 2009-2010, 2015-2016) are clearly visible as years with many recorded episodic drought months across the ~~229~~ 232 sites (Figure 1).

2.4 Meta-analysis

Quantitative drought responses of different plant physiological and ecosystem scale processes were synthesized using meta-analytical statistics. The log response ratio was used as a metric of drought effect size and converted back to percentage change for convenient interpretation. The log response ratio is the natural-log proportional difference between the means in a treatment and a control group (Hedges et al., 1999; Lajeunesse, 2011). In this analysis, we compared measures averaged over wet season months (control) to measures averaged over dry season months (treatment), and in the second comparison the measures averaged over the dry season months (control) with measures averaged over the episodic drought months (treatment) (Figure 3). To be clear, we used only natural drought conditions in the meta-analysis and omitted all data that was acquired in artificial drought experiments. Measurements were ~~often~~ always available in pairs or as repeated measurements (wet season-dry season, dry season-episodic drought), so that the variance of the calculated response ratio has to be adjusted for by the Pearson product correlation coefficient between the measurement pairs (Lajeunesse, 2011). For individual tree measurements, which were available for stomatal conductance, photosynthesis, leaf water potential, tree transpiration and sometimes leaf flushing, the average, standard deviation and correlation coefficient were calculated from the pool of measured trees in each study. When site averages were used, which was the case for all the other measures, the average and standard deviation calculated from the different measurement years were used. The log response ratio and sample variance of the measures in individual studies and sites were calculated using the *escalc* routine and the mean effect sizes and 95% confidence intervals in the *rma* routine, both available in the R package *metafor* (Viechtbauer, 2017).

The variability in magnitude and direction of leaf and tree scale responses to drought were related to the average wood density of the species measured in the different studies. To calculate the average wood density for each study, we created a separate dataset including for each study the genus and species names of the individual trees measured in the study. Preferably, the species-specific wood density was retrieved from the original source. However, if this was not possible, we retrieved wood density from a database of wood properties in neotropical tree taxa collated previously by us (Janssen et al., 2020) or from the global wood density database (Chave et al., 2009b; Zanne et al., 2009). ~~If s~~Species-specific wood density was not available in

128 out of 866 measured individuals~~,~~. For these individuals, the genus averaged wood density was used instead. In neotropical tree taxa, 74% of interspecific variability in wood density can be explained by genus level variability in wood density (Chave et al., 2006). Therefore we consider genus average wood density as a suitable proxy for species level wood density in these cases.~~-~~ Study averaged wood density was used in the *rma* routine from the R package *metafor* (Viechtbauer, 2017) to test whether wood density was a significant moderator variable in the mixed-effect meta-regression model. This model also used inverse-variance weighting of the studies included in the model (Figure 4).

3 Results

3.1 Responses to seasonal drought

The meta-analysis shows that across the measured neotropical forest sites, a dry season decline in relative extractable water (REW) is associated with a decline of soil matric potential in the topsoil (Figure 2 a, c, Figure S3). Furthermore, dry season ~~days~~ months are ~~often less cloudy resulting in higher net radiation,~~characterised by a higher midday air temperature, lower relative humidity and therefore higher vapor pressure deficit (VPD) compared to~~ the~~ wet season months (Figure 1 d, Figure 2 d). As a result of a decline in water supply from the soil and the increase of evaporative demand from the atmosphere, the meta-analysis indicates that across studies, pre-dawn and midday ψ_l both significantly decline from the wet to the dry season (Figure 2 a, Figure 3, a). Pre-dawn ψ_l declines from an average -0.~~22~~ 23 ±0.11 MPa in the wet season to -0.~~34~~ 35 ±0.~~21~~ 28 MPa in the dry season among studies and sites (Figure 2 a). Midday ψ_l declines from an average -0.~~91~~ 89 ±0.~~35~~ 34 MPa to -1.~~32~~ 35 ±0.41 MPa from the wet to the dry season (Figure 2 a). Therefore, the average midday water potential gradient increases from 0.~~69~~ 66 MPa in the wet season to ~~0~~1.~~9~~0~~8~~ MPa in the dry season (Figure 3 b).

The dry season decline of ψ_l triggers progressive stomatal closure resulting in a decline of stomatal conductance and leaf photosynthesis of ~~44~~42% and ~~19~~25% from the wet to the dry season, respectively. However, the data shows no significant decline in potential leaf transpiration from the wet to the dry season (*Random-effects model, p = 0.~~46~~29, n = ~~24~~23*) as the average increase of midday VPD from the wet to the dry season is of the same magnitude as the decline of stomatal conductance (Figure 2 b, d). As the decline in stomatal conductance outweighs the decline in leaf photosynthesis from the wet to the dry season, intrinsic water use efficiency (iWUE) increases by ~~31~~27% from the wet to the dry season (Figure 3, a). Nonetheless, as potential leaf transpiration is sustained in the dry season, actual water use efficiency (WUE) declines by ~~19~~21% from the wet to the dry season (Figure 3, a). These results suggest that on the leaf scale, increased leaf transpiration ~~and a drop in ψ_l~~ in the dry season ~~are~~ is largely prevented by progressive ~~downregulating~~ stomatal ~~conductance~~closure, which is also ~~likely~~ contributing to a decline of leaf photosynthesis.

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The meta-analysis shows that on the tree scale, there is a marginally significant increase of the~~ average~~ water potential gradient ~~is increased~~ while soil to leaf hydraulic conductance is ~~is~~ not significantly reduced from the wet to the dry season (Figure 3 b).

However, crown conductance is significantly reduced by 25% from the wet tot the dry season, suggesting that the increase of atmospheric VPD is offset by a decline in crown conductance that results in no significant change of tree daily transpiration from the wet to the dry season (Figure 3 b). ~~As the increased gradient and reduced conductance are cancelling each other out, there is on average no significant change in daily tree transpiration from the wet to the dry season (Figure 3, b). This is in agreement with the observed sustained dry season transpiration on the leaf scale (Figure 2 a). We observe~~The meta-analysis points to a distinct seasonality of alternating stem and canopy growth (Figure 3, b). The shedding of old and flushing of new leaves during the dry season cumulates into an average 30~~3~~% higher leaf litterfall and ~~32~~26% higher leaf flushing in the dry season, compared to the wet season. While canopy ~~productivity~~ growth increases, average stem diameter growth declines by roughly the same magnitude (~~34~~31%) from the wet to the dry season (Figure 3 b). These results suggest that generally, above-ground productivity alternates between stem and canopy growth from the wet to the dry season.

Despite no observed changes in leaf or tree transpiration, we observed a significant ~~12~~9% increase of ecosystem evapotranspiration from the wet to the dry season (Figure 3 c). Furthermore, the meta-analysis ~~showed a~~also points to a 9% decline in gross ~~ecosystem~~ primary productivity (~~GEP~~GPP)~~ from the wet to the dry season~~, resulting in a significant 19% reduction of ecosystem water-use efficiency ~~-~~from the wet to the dry season (Figure 3 ~~a~~c). Net primary productivity (NPP) declined by 10% from the wet to the dry season, but there was ~~There was also~~ no significant change in above-ground net primary productivity (ANPP) from the wet to the dry season (Figure 3 c). This suggests that primarily root growth declines from the wet to the dry season, while increased canopy growth in the dry season is offset by a decline in stem growth (Figure 4 b). Considering the total ecosystem carbon budget, ~~However, t~~the decline of ~~GEP~~GPP is ~~cancelled out~~offset by a non-significant dry season decline of ecosystem respiration (R_{eco}) resulting in no significant change in net ecosystem productivity (NEP = ~~GEP~~GPP – R_{eco}) from the wet season to the dry season.~~ There was also no significant change in above-ground net primary productivity (ANPP) from the wet to the dry season (Figure 3 c). As GEP is reduced and evapotranspiration increased, ecosystem water-use efficiency is significantly reduced by 19% from the wet to the dry season (Figure 3 c), which is of a similar magnitude as the dry season reduction of WUE on the leaf scale.~~

To test for the sensitivity of the observed responses to our episodic drought definition, we replicated the meta-analysis using a wide and a narrow drought definition, by setting the drought threshold at either 15% or 5% of the driest dry season months, respectively (Methods 2.3). For seasonal drought, changing the threshold did not significantly changed the magnitude or direction of the observed responses (Figure S8 & S9). Slight changes in number of studies included in the analysis contributed to the increase of the water potential gradient from the wet to the dry season becoming not significant anymore when using the wide drought definition (Figure S8 b) while the decline in soil-leaf hydraulic conductance from the wet to the dry season became marginally significant ($p < 0.05$) when using the narrow drought definition (Figure S9 b). These results suggest that the observed responses to seasonal drought in this meta-analysis are robust, that is relatively insensitive to changes in the episodic drought threshold.

3.2 Responses to episodic drought

We found that on average, the number of months per year classified as episodic drought have been increasing since 1979, both in the studied plots (Figure 1 b) as well as across the entire study area (Figure S4).~~driven by a multi-decade decline in dry season soil moisture across the sites.~~ The number of episodic drought months per year increased significantly over time (*r* = 0.62, p < 0.001) and was positively corelated to annual averaged midday air temperature (*r* = 0.82, p < 0.001) and vapor pressure deficit (*r* = 0.88, p < 0.001) indicating both drying and warming over the past four decades (Figure S4, Table S3). Several previously described El Niño related drought events in 1983, 1987, 1997, 2010 and 2015 are superimposed on this trend and clearly visible as years with high midday air temperatures and VPD and relatively many episodic drought months per year (Figure 1 b, d, e, Figure S4).

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Episodic droughts are associated with a higher VPD and a lower ψ_s compared to a regular dry season (Figure 1 d, Figure 2 a, d). Consequently, the pre-dawn ψ_l is on average 0.~~39~~ 32 MPa lower (-0.~~73~~ 67 ±0.~~59~~ 52 MPa) during episodic drought compared to an average dry season (-0.~~34~~ 35 ±0.~~21~~ 28 MPa) (Figure 2 a, Figure ~~4~~ 3 a). Midday ψ_l declines from -1.~~32~~ 35 ±0.41 MPa in the dry season to -1.~~95~~ 8 ±0.~~55~~ 48 MPa during episodic drought, increasing the average water potential gradient by 0.~~24~~ 13 MPa across all measured trees. However, the meta-analysis indicates that this increase is not significant as there is a large variability in the water potential gradient response to episodic drought (Figure ~~4~~3 b).

The decline of midday ψ_l in response to episodic drought is related to a 49~~2~~% reduction of stomatal conductance and ~~25~~27% reduction in leaf photosynthesis compared to a regular dry season (Figure 3~~4~~ a). Contrary to seasonal drought, potential leaf ~~scale~~ transpiration is reduced by an average ~~30~~38% during episodic drought compared to a regular dry season (Figure ~~4~~ 3 a). Similar to seasonal drought, we observe a small increase of ~~This suggests that stomatal downregulation generally outweighs the increased evaporative demand from the atmosphere during episodic drought, effectively limiting leaf transpiration. Furthermore, as stomatal conductance shows a larger magnitude decline in response to episodic drought compared to leaf photosynthesis, WUEi~~iWUE and a decline in WUE in response to episodic drought but these responses are not significant ~~is significantly higher during episodic drought compared to a regular dry season (Figure 4 a). However, leaf transpiration and leaf photosynthesis decline with a similar magnitude in response to episodic drought, so there is no significant change in WUE observed~~ (Figure 4 a).

On the tree scale, there is no significant change in the water potential gradient during episodic drought compared to a regular dry season ~~we observe~~ and also the substantial average decline of 53~~2~~% in soil to leaf hydraulic conductance during episodic drought compared to a regular dry season is not significant (Figure 3 b). Nonetheless, we do observe a significant decline of

36% in crown conductance and a 18% decline of tree daily transpiration in response to episodic drought (Figure 3 b). ~~, associated with an average 21% reduction of daily transpiration (Figure 4 b).~~ Furthermore, stem diameter growth is reduced by an average 6% during episodic drought compared to a regular dry season while leaf flushing and litter fall are not significantly different (Figure 4 d).

On the ecosystem scale, ~~we observe that~~ despite the decline in tree transpiration, the meta-analysis suggests that ~~the observed 4% decline in~~ evapotranspiration during episodic drought is not significantly different to the evapotranspiration in the dry season (*Random-effects model, p = 0.~~47~~63, n = 5*). Furthermore, despite declines in stem growth and leaf photosynthesis during episodic drought (Figure 3 a, b) there are no significant differences in GPP, NPP, ANPP and ecosystem water use efficiency between episodic drought and a regular dry season (Figure 3 c). However, we do observe a significant 9% decline in ecosystem respiration that is driving a 24% increase of net ecosystem productivity in response to episodic drought (Figure 3 c). These results suggest that ecosystem productivity is relatively tolerant to episodic drought while reduced respiration even contributes to a net increase of ecosystem carbon uptake during episodic drought compared to a regular dry season.~~is a small and no significant decline of R_{eco} (-4%), while NEP (+16%), ANPP (+6%) and GEP (6%) show small and no significant increases in response to episodic drought (Figure 4 c). This results in a marginal significant increase of 13% in ecosystem water use efficiency (Figure 4 c).~~

The sensitivity analysis showed that some episodic drought responses are sensitive to changes in the episodic drought threshold, especially on the leaf scale (Figure S8 & S9). When using both the narrow and wide episodic drought definition, the decline in leaf photosynthesis and potential leaf transpiration in response to episodic drought become not significantly different from a regular dry season anymore (Figure S8 a, S9 a). For the narrow definition this is mainly the result of using only half the number of studies compared to the baseline analysis, reducing the statistical power of the test. In the wide definition analysis, the effect size, or the difference between the episodic drought and a regular dry season month, becomes smaller.

3.3 Relationships between study-averaged wood density and drought responses

The meta-analysis revealed ~~a consistent downregulation of~~ that on average, stomatal conductance and leaf photosynthesis are downregulated as pre-dawn and midday ψ_l decline during seasonal and episodic drought. ~~However, the magnitude of these leaf-scale responses to seasonal and episodic drought varies substantially among different studies. W~~Furthermore, we find that between-study variation in the stomatal conductance, leaf transpiration~~,~~ and leaf photosynthesis ~~and midday ψ_l~~ response to seasonal and episodic drought correlates with differences in study-averaged wood density. ~~-~~Generally, studies that measured mainly low wood density tree species showed a stronger response of stomatal conductance~~,~~ and potential leaf transpiration ~~and leaf photosynthesis~~ to seasonal and episodic drought compared to studies that measured mainly high wood density species (Figure ~~5~~4 a, b). ~~Furthermore, t~~The ~~effects of study averaged wood density on the~~ response of leaf photosynthesis to seasonal drought increased ~~midday ψ_l were less clear~~marginally significant ($p < 0.05$) with increasing wood density but this relationship was not visible in response to episodic drought ~~but generally the magnitude of the response increased with wood density~~ (Figure ~~5~~ 4 c~~d~~). There was also no significant effect of wood density on the response of midday ψ_l to seasonal or episodic drought (Figure 4 d) but there was a significant relationship between the episodic drought response of pre-dawn ψ_l and study averaged wood density ($R^2 = 0.76$, $p < 0.05$, not shown). Generally, studies that measured high wood density species showed a stronger decline of pre-dawn ψ_l in response to episodic drought, compared to studies that measured low wood density species. These results suggest that low wood density species are better able to maintain a high pre-dawn ψ_l during episodic drought, possibly because of strong stomatal control on transpiration (Figure 4 a, b) or because of deep soil water accessibility that enables recharging of tissue water at night.

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We find that the response of midday ψ_l to a decline in pre-dawn ψ_l is also strongly dependent on study-averaged wood density (Figure S~~2~~5). Tree species from studies with a high average wood density (> 0.7 g cm^{-3}) showed a strong reduction in midday ψ_l and increase the water potential gradient in response to a decline in pre-dawn ψ_l.~~, which is in accordance with the definition of extreme non-isohydric behavior (sensu Martínez-Vilalta et al., 2014).~~ On the other hand, tree species in studies with a low average wood density species (< 0.5 g cm^{-3}) ~~are characterized by partly isohydric behavior as they~~ show a non-significant decline ~~in~~of midday ψ_l~~the water potential gradient~~ in response to a decline in pre-dawn ψ_l. Studies with intermediate average wood density (0.5-0.7 g cm^{-3}) show~~ an intermediate response with~~ a decline of midday ψ_l ~~declining~~ parallel to a decline in pre-dawn ψ_l (slope ~1) ~~suggesting strictly non-isohydric behavior~~ (Figure S2). Related to these results we found that the stomatal response to atmospheric VPD also depends on study-averaged wood density, with low wood density species showing strong stomatal downregulation in response to increased atmospheric VPD, while no stomatal downregulation is observed in high wood density species (Figure S~~6~~3). These results imply that low wood density species prevent a midday drop in ψ_l during seasonal and episodic drought by downregulating stomatal conductance, leaf transpiration and photosynthesis in response to elevated midday VPD, while high wood density tree species keep a more variable ψ_l and have no strong stomatal control on leaf transpiration.

The dry season responses of the two tree-scale measures for which enough species-specific data was available, tree daily transpiration and leaf flushing, also showed significant relationships with study-averaged wood density (Figure 4 e, f~~6~~). The relationship between study-averaged wood density and the magnitude of the seasonal drought response of tree daily transpiration was similar in terms of magnitude and direction as the relationship between wood density and~~ with~~ the leaf transpiration response (Figure ~~5~~4 b, Figure ~~6~~4 e~~a~~). Roughly half of the studies that measured mainly low wood density species showed a dry season decline in tree transpiration. The other half of the studies that measured mainly high wood density species showed a dry season increase of tree transpiration (Figure ~~6 ~~4 ~~a~~e). Similarly, dry season leaf flushing is found to be more pronounced in high wood density species compared to low wood density species that actually show on average a decline of leaf flushing in the dry season (Figure 4,~~6 b~~f). Finally we find that study-averaged stomatal conductance, leaf photosynthesis, midday ψ_l, tree daily transpiration, soil-leaf hydraulic conductance and crown conductance all significantly decline with increasing study-averaged wood density (Figure S7). These results suggest that low wood density species, compared to high wood density species, are characterized by efficient water transport, high stomatal conductance and leaf photosynthesis during the wet season but also show a strong decline of stomatal conductance, transpiration and photosynthesis in response to drought.

4 Discussion

4.1 How do leaf, tree and ecosystem scale processes respond to seasonal drought?

Stomatal behaviour and changes in soil to leaf hydraulic conductance determine the ~~hydrological~~ hydraulic response to seasonal drought in neotropical trees, driving tree transpiration and ecosystem evapotranspiration (Figure 2 & 3). The downregulation of stomatal conductance and ~~soil to leaf hydraulic~~canopy conductance in the dry season is a widely observed ~~hydrological~~ hydraulic response to a decline in leaf and xylem water potential (Fisher et al., 2006; Machado and Tyree, 1994; Williams et al., 1998). However, progressive ~~S~~stomatal closure is ~~cancelled out~~offset by a higher midday VPD in the dry season resulting in no observed change in potential leaf transpiration from the wet to the dry season across studies (Figure 3 a). Similarly, the dry season decline in hydraulic conductance and crown conductance is ~~cancelled~~ offset~~out~~ by an increase of the water potential gradient (midday ψ_l - pre-dawn ψ_l) within the tree and the increase of midday VPD, resulting in no average change in tree daily transpiration from the wet to the dry season across studies (Figure 3 b). The decline of soil to leaf hydraulic conductance in the dry season is the result of embolism formation in the xylem vessels that reduces xylem hydraulic conductance (Bonal et al., 2000a; Fontes et al., 2018; Machado and Tyree, 1994; Meinzer et al., 2008b). Our data did not allow us to disentangle whether dry season transpiration is mainly constrained by a decline in ~~stomatal~~ stomatal conductance or a decline in soil to leaf hydraulic conductance. However, the decline of hydraulic conductance and stomatal conductance with decreasing xylem water potential are strikingly similar (Brodribb et al., 2003) suggesting that xylem hydraulic vulnerability and stomatal sensitivity are strongly coordinated (Fontes et al., 2018; Maréchaux et al., 2018; Meinzer et al., 2008b).

The meta-analysis suggests that the dry season downregulation of stomatal conductance is accompanied by a smaller but significant decline in leaf photosynthesis (Figure 3 a). Therefore, the leaf-scale intrinsic water use efficiency (~~WUEi~~iWUE) increases on average from the wet to the dry season (Figure 3 a). This increase of ~~WUEi~~iWUE in the dry season was also found in earlier site-specific studies (Bonal et al., 2000a; Hogan et al., 1995; Santos et al., 2018). We~~We~~ also find that sustained leaf transpiration in the dry season is resulting in a decline of actual leaf water use efficiency (WUE) from the wet to the dry season (Figure 3 a). Furthermore, as gross ~~ecosystem~~ primary productivity (~~GEP~~GPP) declines and evapotranspiration increases, we also observe a decline of ecosystem water use efficiency from the wet to the dry season (Figure 3 c). Therefore, our results suggests that despite a decline in stomatal conductance, neotropical forests become less water efficient in the dry season. This is in agreement with a global synthesis of eddy-covariance measurements that showed that humid tropical forests show a decline of ecosystem water use efficiency in response to drought (Yang et al., 2018a).

~~Our~~ The meta-analysis results show that across neotropical forests, ~~above-ground~~ net primary productivity (~~A~~NPP) declines while above-ground NPP (ANPP) does not change from the wet to the dry season (Figure 3 c). This suggests that the decline in total NPP is primarily the result of a decline in root growth in the dry season, confirming earlier findings that root growth declines with a decline in soil moisture in the dry season (Girardin et al., 2016; Metcalfe et al., 2008). Furthermore, we find that above-ground growth is shifted from the stem in the wet season to the canopy in the dry season (Figure 3 b) without changes in overall above-ground growth. Finally, the meta-analysis shows that the dry season decline of GPP is offset by the decline of ecosystem respiration, resulting in no significant change in net ecosystem productivity from the wet to the dry season (Figure 3 c). The dry season decline of ecosystem respiration is likely driven by a decline of heterotrophic respiration from the soil and litter layer as soil and litter respiration is found to be strongly dependent on the availability of moisture in neotropical forests (Chambers et al., 2004; Sotta et al., 2004; Zanchi et al., 2014). ~~Furthermore, our meta-analysis suggests that on average GEP is reduced in the dry season compared to the wet season (Figure 3 c) indicating that above-ground carbon use efficiency (ANPP / GPP) is increased in the dry season. The increase of carbon use efficiency might be explained by a relative dry season decline of autotrophic respiration (Doughty et al., 2015b; Rowland et al., 2014) that is driven by a decline in stem respiration (del Aguila-Pasquel et al., 2014; Nepstad, 2002). Alternatively, a dry season decline of carbon allocation towards the roots might explain why a decline in GEP does not result in an apparent decline of above-ground growth (Girardin et al., 2016).~~

~~Another explanation is that in the dry season, stored non-structural carbohydrates (NSC's) are utilized for canopy growth. Previous work suggests that NSC concentrations in neotropical trees are not reduced in response to seasonal and episodic drought (Dickman et al., 2019; Würth et al., 2005). This implies that temporary reductions in photosynthesis and gross productivity are not sufficient to limit actual tree growth in the dry season (Würth et al., 2005).~~ ~~In summary, the observed seasonal drought responses related to stomatal and hydraulic conductance, transpiration and photosynthesis occur on relatively short time-scales of hours and days and are therefore adequately captured by our approach. However, tree and ecosystem scale responses related to productivity, carbohydrate status and growth allocation operate on seasonal to multi-annual timescales which do not always correspond with the observations on the leaf scale and might not be fully captured by our meta-analysis.~~

4.2 How do leaf, tree and ecosystem scale processes respond to episodic drought?

Episodic droughts seem to have become more common in South and Central America recently. ~~.~~Previously classified as once in a century episodic droughts are now occurring roughly every five years (Aragão et al., 2007; Coelho et al., 2012; Erfanian et al., 2017; Marengo et al., 2008, 2011; Panisset et al., 2017). Furthermore, ENSO ~~swings~~extremes that are clearly linked to major droughts in neotropical forests (Figure 1, Figure S4) have been intensifying in the 20th and 21st century (Grothe et al., 2019). Following our definition of episodic drought, we observe a significant increase of the number of episodic drought months per year ~~occurrence~~ since 1979, both across the ~~229~~ 232 neotropical forest sites ~~since 1979~~ (Figure 1 b) as well as across the entire humid neotropical forest biome (Figure S4). This result is in agreement with the analysis of alternative datasets indicating that dry seasons in Amazonia have been becoming dryer since 1979 (Fu et al., 2013). The mechanisms driving this dry season drying are uncertain but have been attributed to changes in global atmospheric circulation (Fu et al., 2013) and more regionally to deforestation (Costa and Pires, 2010; Debortoli et al., 2017). We also find that midday air temperature and VPD have been increasing over the same period (Figure S4), suggesting that episodic drought have not only become more frequent but also hotter since 1979. ~~Furthermore, ENSO swings that are clearly linked to major droughts in neotropical forests (Figure 1) have been intensifying in the 20th and 21st century (Grothe et al., 2019).~~ In this meta-analysis, we were able to use leaf, tree and ecosystem scale data from five major episodic drought years, namely from 1987, 1997, 2005, 2010 and 2015 (Figure 1).

Episodic droughts reduce the supply of water from the soil and increase the evaporative demand of the atmosphere beyond values that are observed in a regular dry season (Figure 2) (see also Jiménez-Muñoz et al., 2016; Lee et al., 2013; Panisset et al., 2017). We find that both stomatal conductance, leaf transpiration and photosynthesis are reduced ~~and WUEi is increased~~ during episodic drought compared to a regular dry season (Figure 3~~4~~ a). This suggests that the physiological responses to episodic drought on the leaf level are, in terms of direction and magnitude, a continuation of the seasonal drought response~~s observed~~. Stomatal limitations may explain the observed decline of leaf photosynthesis in response to episodic drought, as changes in nutrient or chlorophyll concentrations were not reported for the 2015 drought in the central Amazon (Santos et al., 2018). Alternatively, reductions in carboxylation capacity and mesophyll conductance in response to leaf desiccation or high leaf temperatures could cause a more permanent reduction of photosynthesis during episodic drought (Dewar et al., 2018; Doughty, 2011; Felsemburgh, 2009; Lloyd and Farquhar, 2008; Zhou et al., 2013). The average midday ψ_l observed during episodic drought (-1.8 MPa) induces leaf turgor loss in many tropical rainforest trees (Maréchaux et al., 2015). The importance of tissue desiccation and heat-induced damage to the photosynthetic machinery is presently not known but could become increasingly important in the tropical carbon cycle in a warmer climate.

-The sensitivity analysis shows that these leaf-scale responses are sensitive to changes in the episodic drought threshold (Figure S8, S9). Choosing a wide drought definition (15% of the driest dry season months) results in that the difference between a regular dry season and episodic drought disappears (Figure S8), while choosing a narrow drought definition (5% of the driest dry season months) results in a great loss of data points and therefore the statistical power of the test (Figure S9). Choosing an arbitrary episodic drought threshold to compare a regular dry season with an episodic drought will always result in uncertainties of the observed responses. However, after testing the sensitivity of the episodic drought threshold we conclude that most of the observed responses to seasonal and episodic drought are robust, while highlighting the importance of choosing an episodic drought threshold that is strict enough (i.e. only includes exceptionally dry conditions) while it still yields a large enough sample size for the statistical analysis to differentiate.

~~Stomatal limitations may explain the observed decline of leaf photosynthesis, as changes in nutrient or chlorophyll concentrations were not reported for the 2015 drought in the central Amazon (Santos et al., 2018). Alternatively, reductions in carboxylation capacity and mesophyll conductance in response to leaf desiccation or high leaf temperatures could cause a more permanent reduction of photosynthesis during episodic drought (Dewar et al., 2018; Doughty, 2011; Felsemburgh, 2009; Lloyd and Farquhar, 2008; Zhou et al., 2013). The average midday~~ ψ_t ~~observed during episodic drought (-1.95 MPa) induces leaf turgor loss in many tropical rainforest trees (Maréchaux et al., 2015). The importance of tissue desiccation and heat-induced damage to the photosynthetic machinery is presently not known but could become increasingly important in the tropical carbon cycle in a warmer climate.~~

~~Another explanation is that in the dry season, stored non-structural carbohydrates (NSC's) are utilized for canopy growth. Previous work suggests that NSC concentrations in neotropical trees are not reduced in response to seasonal and episodic drought (Dickman et al., 2019; Würth et al., 2005). This implies that temporary reductions in photosynthesis and gross productivity are not sufficient to limit actual tree growth in the dry season (Würth et al., 2005).~~

~~We observe~~The meta-analysis results suggests that ~~reductions of~~ stem growth is significantly reduced during episodic drought while leaf litter fall and leaf flushing do not show a consistent positive or negative change ~~in response to episodic drought~~ (Figure 3 b). The decline of stem growth during episodic drought is widely observed across tropical humid forests and has been linked to a temporary decline in tropical forest carbon sink (Brienen et al., 2015; Clark et al., 2003, 2018; Feldpausch et al., 2016; Rifai et al., 2018). However, declines in stem growth are not always obvious (Doughty et al., 2014, 2015; Phillips et al., 2009) and are at some sites compensated for by an increase in canopy growth or root growth (Doughty et al., 2015; Hofhansl et al., 2014) resulting in no observed net change in NPP or ANPP during episodic drought (Figure 3 c). These results suggest that despite significant reductions in leaf photosynthesis during episodic drought, overall tree growth is not limited by ~~The observed reduction of stem growth is not likely related to reductions in~~ carbohydrate availability (carbon starvation) (Mcdowell et al., 2008; Sala et al., 2012). ~~as r~~ Recent evidence from neotropical humid forests suggests that leaf and wood tissue concentrations of non-structural carbohydrates (NSC's)~~NSCs~~ are kept relatively constant during seasonal and severe episodic drought (Dickman et al., 2019; Würth et al., 2005). ~~-~~This implies that temporary reductions in photosynthesis are not sufficient to limit actual tree growth during drought (Würth et al., 2005). ~~Alternatively,~~The significant decline in stem growth in response to episodic drought ~~-~~is more likely ~~limited~~driven by cell turgor loss in the vascular cambium as a result of tissue desiccation, which limits cell formation and thus the formation of new tissue in the stem (Körner and Basel, 2013; Krepkowski et al., 2011; Muller et al., 2011). It is essential to understand which mechanisms, turgor mediated, carbon mediated, or a combination of both, are driving drought-induced declines in stem growth, as they can operate on different time scales and can have different sensitivities to drought.

4.3 What are the differences between seasonal and episodic drought?

We find that the responses of stomatal conductance, leaf photosynthesis, midday and pre-dawn ψ_l to episodic drought are basically a continuation of the same leaf physiological responses observed during seasonal drought (Figure ~~3~~2 & 4~~3~~). However, unlike seasonal drought, the decline in stomatal conductance and crown conductance outweighs the increase of atmospheric VPD during episodic drought, effectively reducing ~~leaf~~ transpiration~~. Similarly, the additional embolism-induced reduction of soil to leaf hydraulic conductance outweighs the increase of the water potential gradient within the tree, causing a reduction of tree daily transpiration during episodic drought compared to a regular dry season~~ (Figure 4 a, b). Our results are in agreement with site-specific observations that tree daily transpiration is reduced through a combination of stomatal downregulation and a loss of soil to leaf hydraulic conductance, both in response to episodic drought (Fontes et al., 2018) and multi-year drought (Fisher et al., 2006). Unlike the rapid recovery of stomatal conductance, soil to leaf hydraulic conductance has been observed not to recover fully after episodic drought (Fontes et al., 2018) imposing a legacy effect on transpiration in the first months following episodic drought. Furthermore, the loss of hydraulic conductance might be considered an early warning signal for embolism-induced drought mortality (Rowland et al., 2015b) following episodic drought (Feldpausch et al., 2016; Phillips et al., 2009).

Contrary to seasonal drought, we observe no increase in leaf flushing and litterfall and no significant declines in NPP and ~~R_{eco} and GEP~~GPP during episodic drought. One explanation for this apparent discrepancy is that leaf flushing, litterfall, NPP and ~~GEP~~GPP operate on seasonal timescales and are strongly dependent on tree phenology. Most neotropical tree species shed old and flush new leaves during the dry season as their leaf phenology is synchronized to maximum daily insolation (Borchert et al., 2015; Bradley et al., 2011; Brando et al., 2010; Graham et al., 2003; Wagner et al., 2016; Wright and van Schaik, 1994). This results in an initial decline followed by a progressive increase of photosynthetic capacity on the ecosystem scale in the late dry season as leaves mature (Albert et al., 2018; Doughty and Goulden, 2009b; Wu et al., 2016). Leaf flush and maturation, and with it the increase of leaf photosynthetic capacity, drive a progressive increase of ~~GEP~~GPP during the dry season in humid neotropical forests (Albert et al., 2018; Araújo et al., 2016; Doughty and Goulden, 2009b; Hutyra et al., 2007; Restrepo-Coupe et al., 2013). Episodic droughts by our definition always occur at the end of the dry season, when REW is lowest (Figure 1). Therefore, the peaks in litter fall and leaf flush that generally occur in the first half of the dry season, have already occurred before the episodic drought starts and therefore ~~GEP~~GPP is relatively high. We hypothesize that the seasonal timescales of tree phenology and ecosystem productivity could be counteracting the potential negative effects of short episodic droughts on ~~GEP~~GPP, which were therefore not observed in the meta-analysis.

4.4 ~~What are observed inconsistencies in leaf, tree and ecosystem scale responses~~How do we scale from the leaf to the ecosystem?

Our meta-analysis indicates a general tendency of seasonal and episodic drought responses becoming smaller and not significant when going from the leaf and tree scale to the ecosystem scale. Regarding transpiration, we observed sustained leaf and tree scale transpiration in the dry season ~~(Figure 3)~~ and a decline of leaf and tree scale transpiration in response to episodic drought (Figure 3~~4~~). In contrast, ecosystem evapotranspiration increases significantly in the dry season ~~(Figure 3 c)~~ and does not significantly change during episodic drought (Figure ~~4~~3 c). This discrepancy is not logically explained by an increased contribution of evaporation from the soil and canopy to evapotranspiration, as both soil and canopy evaporation are expected to be lower in the dry season and during episodic drought compared to the wet season (Shuttleworth, 1988).

A more likely explanation is that the leaf and tree-scale data used in our meta-analysis are biased towards fast-growing pioneer tree species with low wood density that are growing in upper canopy positions (e.g. Dünisch and Morais, 2002; Huc et al., 1994; Kunert et al., 2010; Machado and Tyree, 1994). Stomatal control on transpiration is stronger in low wood density compared to high wood density tree species (Figure ~~5 & 6~~4, Figure S~~2~~6). Furthermore, sun-exposed trees in upper canopy positions experience a higher evaporative demand from the atmosphere, resulting in a more pronounced downregulation of stomatal conductance and photosynthesis in response to seasonal and episodic drought compared to understory trees (Domingues et al., 2014; Fisher et al., 2006; Santos et al., 2018). This sample bias in the meta-analysis might also explain why ecosystem scale responses of ~~water and~~ carbon exchange to drought ~~to episodic drought~~ seem to contradict the observations on the leaf and tree scale. The decline of ~~L~~leaf photosynthesis is more than twice the magnitude of the decline in GPP during seasonal drought, while in response to episodic drought there is not even a decline in GPP detected (Figure 3). ~~and stem growth are observed to significantly decline while GEP and ANPP show a small and not significant increase in response to episodic drought (Figure 4).~~ This meta-analysis result is confirmed by unexpected results from ~~site-specific~~previous studies that found that ~~GEP~~GPP and ~~A~~NPP are not reduced during episodic drought ~~(Bonal et al., 2008)~~ despite significant declines of leaf photosynthesis (Bonal et al., 2008; Doughty et al., 2014, 2015).

Another explanations for the apparent contradiction between leaf, tree and ecosystem scale responses to episodic drought is the limited timescale on which we analysed ecosystem drought responses. The temporal scale of some tree and ecosystem scale responses to episodic drought might extend far beyond the actual drought (e.g. Gonçalves et al., 2020; Hofhansl et al., 2014). For example, episodic drought events have been found to elevate tree mortality rates across neotropical forests (Condit et al., 1995; Feldpausch et al., 2016; Phillips et al., 2009; Williamson et al., 2000). Tree mortality can significantly impact ecosystem productivity and transpiration, carbon storage and canopy structure, impacting the understory light environment and microclimate for many years (da Costa et al., 2018; Leitold et al., 2018; Rice et al., 2004, 2008; Rowland et al., 2018; Saatchi et al., 2013; Yang et al., 2018a). Furthermore, extensive leaf flushing in the first months after an episodic drought have been reported (Doughty et al., 2014, 2015; Gonçalves et al., 2020; Hofhansl et al., 2014) contributing to ANPP exceeding predrought values in the years directly following episodic drought (Doughty et al., 2014, 2015; Hofhansl et al., 2014). These legacy effects of drought are not captured by or meta-analysis, which is a limitation of the method used. Therefore, we were unable to grasp the complete, or final extent of the tree and ecosystem scale responses to episodic drought.

4.5 How is wood density related to leaf and tree scale responses to drought?

The meta-analysis shows that the magnitude and direction of the stomatal conductance, leaf photosynthesis, leaf and tree-scale transpiration and leaf flushing response to seasonal ~~and episodic~~ drought is strongly related to the wood density of trees measured in a particular study (Figure ~~5 & 6~~4). The same relationship was observed for stomatal conductance and leaf scale transpiration in response to episodic drought (Figure 4). Generally, we find that studies that measured tree species with a relatively low wood density showed a ~~more isohydric and~~ drought avoiding response, including strong stomatal control on transpiration and no dry season leaf flushing (Figure ~~5 & 6~~4). Conversely, studies that measured tree species with a relatively high wood density showed no stomatal downregulation, increased leaf and tree-scale transpiration and increased leaf flushing in the dry season (Figure ~~5 & 6~~4). As a result, high wood density trees show a stronger desiccation of the leaves and stem during drought and a lower midday leaf and xylem water potential (Figure ~~5 c, d~~S5 & S7) (Borchert, 1994; De Guzman et al., 2017; Meinzer et al., 2008b; Sterck et al., 2014). Wood density appears a good proxy of hydraulic behaviour and could well be used to predict responses of stomatal conductance, transpiration and leaf flushing to seasonal and episodic drought (see e.g. Christoffersen et al., 2016).

Differences in wood density among tree species have been widely studied and are linked to differences in plant hydraulic properties such as hydraulic conductance, sapwood capacitance and embolism resistance (Baas et al., 2004; Chave et al., 2009a; Janssen et al., 2020; Poorter et al., 2010). The use of wood density as a proxy of more fundamental hydraulic properties has been criticized as it often lacks a functional basis (Lachenbruch and Mcculloh, 2014; Patiño et al., 2012). Sapwood capacitance, the amount of water released from the xylem under a certain pressure, is arguably the only hydraulic property that is functionally related to wood density, as the amount of space available for water storage in the wood scales inversely with wood density (Janssen et al., 2020; Meinzer et al., 2008b; Poorter, 2008; Pratt and Jacobsen, 2017; Ziemińska et al., 2019). Sapwood capacitance ~~is~~is positively related to maximum stomatal conductance, leaf photosynthesis, transpiration, soil to leaf hydraulic conductance and midday ψ_l (Meinzer et al., 2003; Oliva Carrasco et al., 2015; Santiago et al., 2004). We show that these relationships hold when relating not species but study-averaged wood density, as a proxy of sapwood capacitance, to study-averaged stomatal conductance, leaf photosynthesis, daily transpiration, midday ψ_l ~~an~~, crown conductance and ~~d~~ soil to leaf hydraulic conductance (Figure S74). Our results suggest that wood density, via sapwood capacitance, is largely driving the magnitude of the stomatal and transpiration response to seasonal and episodic drought in neotropical trees.

The difference in hydraulic behaviour between low and high wood density tree species is confirmed by the observation that the decline of stomatal conductance with atmospheric VPD and the slope of the relationship between midday ψ_l and pre-dawn

ψ_l are strongly dependent on wood density (Figure S~~2~~5 & S~~3~~6). We find that low wood density trees with high sapwood capacitance show a relatively high maximum soil to leaf hydraulic conductance as stored water is used for transpiration (Figure S7~~4~~) while stomatal conductance is downregulated with increasing VPD in the dry season to avoid dehydration (Figure S~~3~~6) (Goldstein et al., 1998; Meinzer et al., 2004, 2008b). Conversely, in high wood density trees, transpiration is primarily constrained by the relatively low soil to leaf hydraulic conductance all year around and stomatal downregulation plays a minor role. High wood density trees maintain stomatal conductance (0.07 – 0.14 mol m^{-2} s^{-1}) even during severe episodic drought (Alexandre, 1991; Bonal et al., 2000a; Roberts et al., 1990; Santos et al., 2018; Stahl et al., 2013b). This implies that transpiration has to increase during seasonal and episodic drought in high wood density trees, resulting in a significant decline of midday ψ_l (Figure 4, Figure S~~2~~5) (Alexandre, 1991; Bonal et al., 2000a; Brum et al., 2019; Domingues et al., 2014).

~~These results present a contradiction to remote sensing data that suggests that neotropical humid forests are strictly isohydric (Konings and Gentine, 2017). At least at the leaf level, most neotropical trees in this meta-analysis and especially high wood density trees show non-isohydric behaviour (Figure S2). Following the definition of Martinez-Vilalta et al. (2014): the water potential gradient generally increases with a decline in pre-dawn ψ_l in response to seasonal and episodic drought (Figure 3 & 4, Figure S2).~~ The observed insensitivity of stomatal conductance to VPD in high wood density trees has been reported previously for lowland rainforest species (Bonal et al., 2000a; Domingues et al., 2014; Granier et al., 1992; Huc et al., 1994) and for tree species of tropical montane cloud forest (Rada et al., 2009). Stomatal insensitivity to VPD is a possible adaptation to surviving in a humid and deeply shaded understory, as the CO_2 concentration inside the leaf is kept high to maximize photosynthesis during brief moments of high irradiance, known as sun flecks (Domingues et al., 2014; Pons et al., 2005; Tinoco-Ojanguren and Pearcy, 1992).

The capability to maintain stomatal conductance and transpiration during short episodic droughts has been explained by the uptake of deep soil moisture using tap roots (Bonal et al., 2000a; Brum et al., 2019; Meinzer et al., 1999; Nepstad et al., 1994; Stahl et al., 2013a, 2013b). Soil water at a depth of up to 18 meters was found to be accessible for trees at Tapajós in the eastern Amazon (Davidson et al., 2011), enabling trees to maintain a favourable water status during short dry periods. This also becomes clear from the relatively high average pre-dawn ψ_l during episodic drought (-0.~~73~~ 67 MPa), compared to tree species of tropical dry forest where pre-dawn ψ_l can approach -2.5 MPa in a regular dry season, inducing leaf wilting and high mortality rates in tree seedlings (Sobrado, 1986; Veenendaal et al., 1996). Soil depth, root functioning and differences in root architecture are believed to be crucial regulators during drought (Brum et al., 2019; Meinzer et al., 1999; Stahl et al., 2013a), but lack of data in neotropical forests prevented us from including these traits in our meta-analysis.

Deep soil moisture uptake is not always sufficient to maintain a favourable water status within the tree as drought-induced tree mortality events have been widely observed across the neotropics (Condit et al., 1995; Feldpausch et al., 2016; Phillips et al., 2009; Williamson et al., 2000), likely resulting from hydraulic failure (Rowland et al., 2015b). The effect of an increased evaporative demand during drought should not be overlooked, as a high VPD can trigger xylem embolism in trees even when soil water is still easily accessed (Fontes et al., 2018; Phillips et al., 2001). Moreover, our results point to the lack of drought avoidance in high wood density tree species as stomatal conductance and transpiration are sustained under high evaporative demand, resulting in a strong decline of xylem and leaf water potential during drought (Figure 4~~5 & 6~~, Figure S~~2~~5 & S6). However, many high wood density tree species in humid neotropical forests have evolved in permanently wet environments and are not always tolerant against xylem embolism (Janssen et al., 2020; Powell et al., 2017; Santiago et al., 2018). The combination of relatively low sapwood capacitance, limited stomatal control on transpiration and limited embolism resistance can amount to high drought-induced mortality rates in some of these high wood density tree taxa (Janssen et al., 2020). This highlights the fact that a lack of properties contributing to drought avoidance in a particular individual or species are not always compensated for by a high drought tolerance, making this individual or species highly vulnerable to drought-induced mortality.

5 Conclusions

In this study, we performed a meta-analysis that provides a quantitative overview of leaf, tree and ecosystem responses to seasonal and episodic drought in neotropical humid forest. We find that the observed leaf-scale responses to episodic drought are a continuation of the responses observed during seasonal drought: reductions in leaf water potential, stomatal conductance and photosynthesis. The observed dry season decline in stem growth and increases of leaf flushing and litter fall seem to be unrelated to water stress~~, as is assumed in most land surface models (LSMs).~~. Rather, the seasonal oscillation of growth allocation between stem and canopy seems to be driven by tree phenology which is synchronised to maximum incoming solar radiation in the dry season.~~-~~ Drought responses related to stomatal and hydraulic conductance, transpiration and photosynthesis are adequately captured by our approach because these responses occur on relatively short time-scales of hours and weeks with the opening and closure of leaf stomates, the occurrence of xylem embolism and the flushing of new leaves. However, tree and ecosystem scale responses related to productivity and growth allocation are also dependent on carbohydrate status which operates on seasonal to multi-annual timescales. The meta-~~-~~analysis confirms that the variability and magnitude of drought responses decline when going from the individual leaf to the ecosystem level in highly diverse tropical forests. Biodiversity driven dynamics at the community level, such as niche partitioning, likely contribute to ecosystem resistance and resilience in response to episodic drought. Finally, we found that wood density, via its direct relationship with sapwood capacitance, acts as a good proxy of hydraulic behaviour and largely explains the magnitude of stomatal and transpiration responses to seasonal and episodic drought.~~ The results presented in this study can act as a response-benchmark for LSM simulations~~

Data availability

The data compiled for this study and used in the meta-analysis is available at https://hdl.handle.net/10411/41KALW

Author contribution

T.J., S.L. and H.D. designed the research, T.J., K.F., S.L., K.N. and H.D. coordinated the writing and contributed ideas, T.J. compiled the database and analysed the data, K.F., S.L., K.N. and H.D. assisted with writing the final manuscript

Competing interests

The authors declare that they have no conflict of interest

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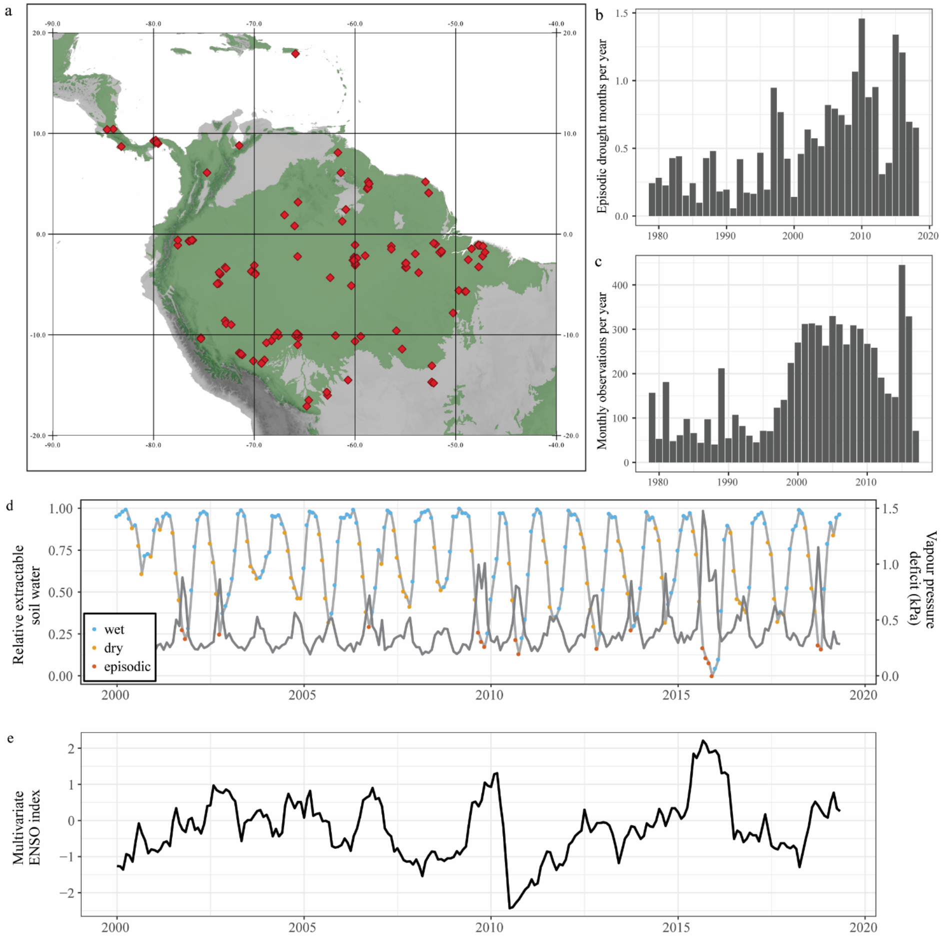
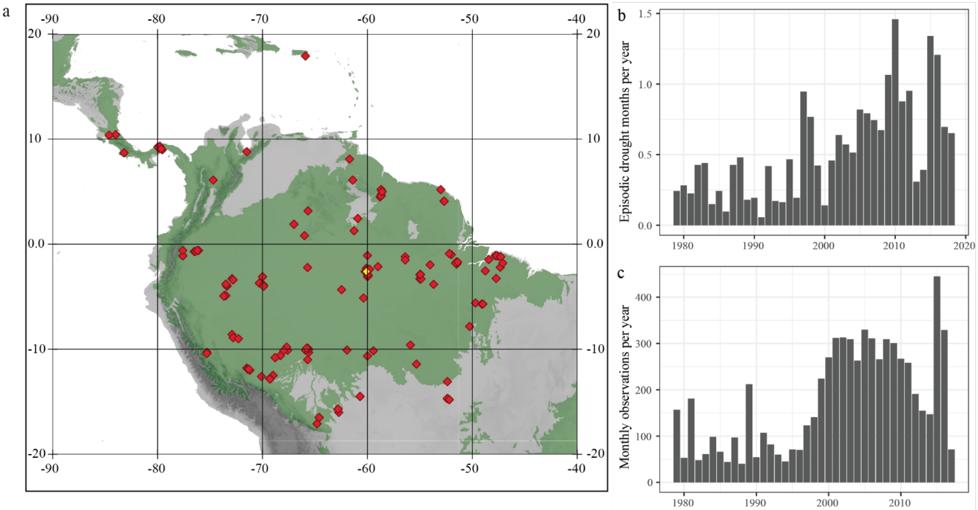
Figures


a
-90.0
-80.0
-70.0
-60.0
-50.0
-40.0
20.0
10.0
0.0
-10.0
-20.0
b
Episodic drought months per year
0.0
0.5
1.0
1.5
1980
1990
2000
2010
2020
c
Monthly observations per year
0
100
200
300
400
1980
1990
2000
2010
d
Relative extractable soil water
0.00
0.25
0.50
0.75
1.00
Vapour pressure deficit (kPa)
0.0
0.5
1.0
1.5
wet
dry
episodic
2000
2005
2010
2015
2020
e
Multivariate ENSO index
−2
−1
0
1
2
2000
2005
2010
2015
2020



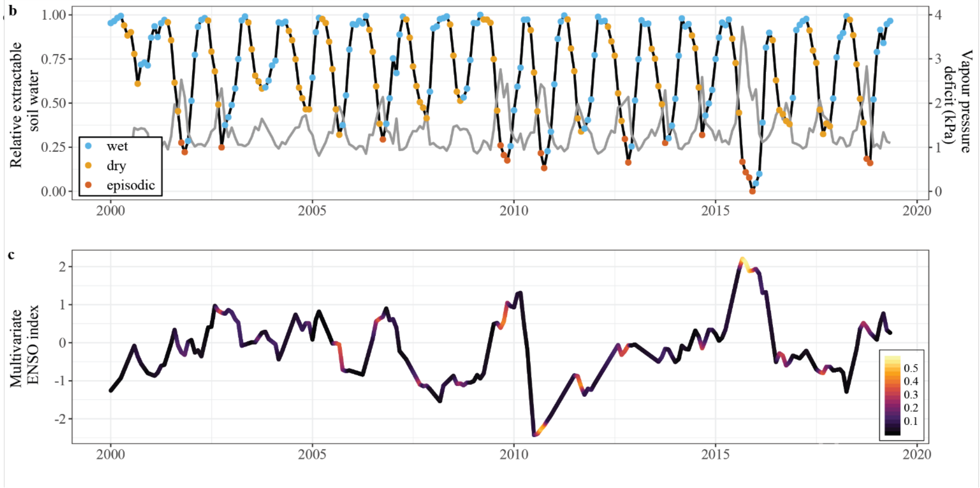
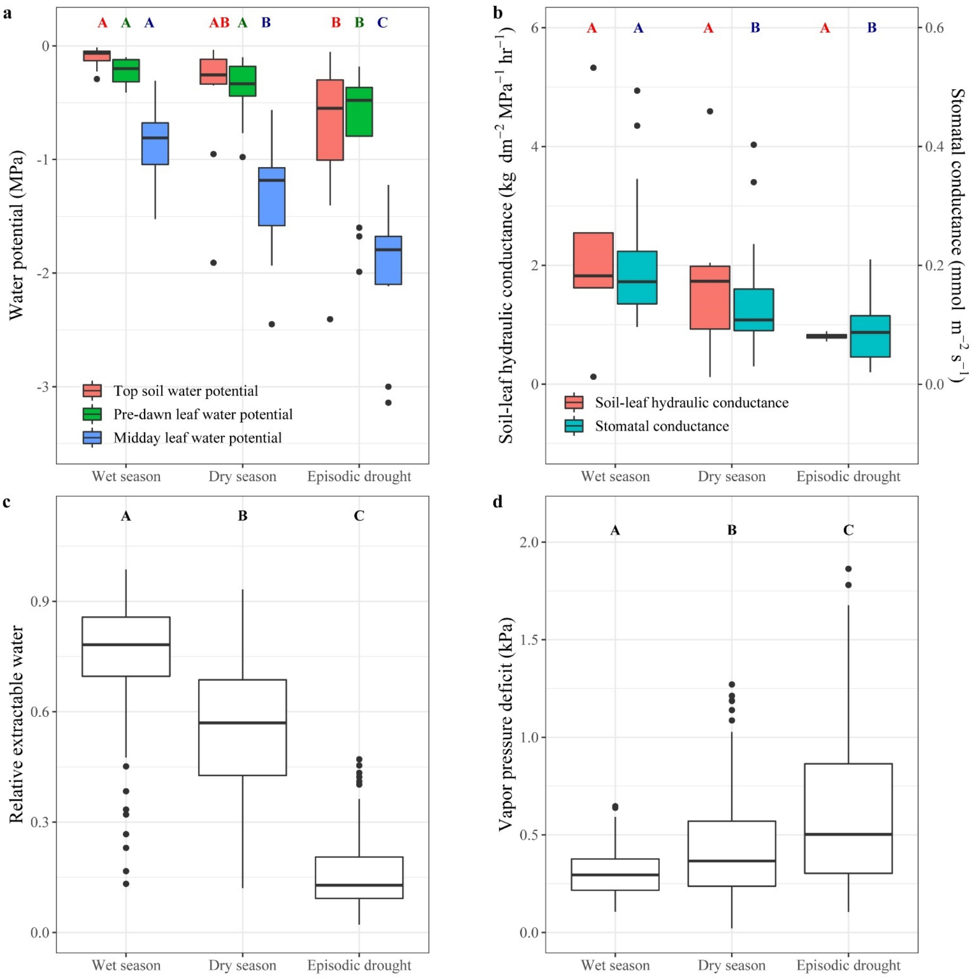


Figure 1: Summary of the database. Site locations (a), average number of episodic drought months ~~recorded per site~~ per year (b) and number of monthly observations in the database per year (c). The map shows the locations of the 229 neotropical forest sites from which data was used in this meta-analysis. In green, the distribution of tropical and subtropical moist broadleaf forest from the terrestrial ecoregions of the world map (Olson et al. 2001). The average number of episodic drought months per year (b) was calculated as the average number of months classified as episodic drought per year recorded at all sites, independent of whether we

have field data for these months. Below, a monthly time-series of relative extractable water (light grey) and vapour pressure deficit (dark grey) for the K34 site in the central Amazon (d), indicated in yellow on the map (a). ~~and the multivariate ENSO index (e).~~The coloured dots indicate whether that specific month was classified as a wet season, dry season or episodic drought month. (e) shows a timeseries of ~~-~~the multivariate ENSO index with positive values indicating El Niño (dry) conditions and negative values La Niña (wet) conditions. The colouring of the ENSO index represent the number of episodic drought months recorded per month at each site in the database, ranging from 0 (no droughts recorded) to 0.58 (episodic drought in 58% of the plots). ~~The map shows the locations of the 229 neotropical forest sites from which data was used in this meta-analysis. In green, the distribution of tropical and subtropical moist broadleaf forest from the Terrestrial ecoregions of the world map (Olson et al. 2001).~~

a
A A A
AB A B
B B C
Water potential (MPa)
0
-1
-2
-3
Top soil water potential
Pre-dawn leaf water potential
Midday leaf water potential
Wet season
Dry season
Episodic drought
b
A A
A B
A B
Soil-leaf hydraulic conductance (kg dm^{-2} MPa^{-1} hr^{-1})
Stomatal conductance (mmol m^{-2} s^{-1})
6
4
2
0
0.6
0.4
0.2
0.0
Soil-leaf hydraulic conductance
Stomatal conductance
Wet season
Dry season
Episodic drought
c
A
B
C
Relative extractable water
0.9
0.6
0.3
0.0
Wet season
Dry season
Episodic drought
d
A
B
C
Vapor pressure deficit (kPa)
2.0
1.5
1.0
0.5
0.0
Wet season
Dry season
Episodic drought

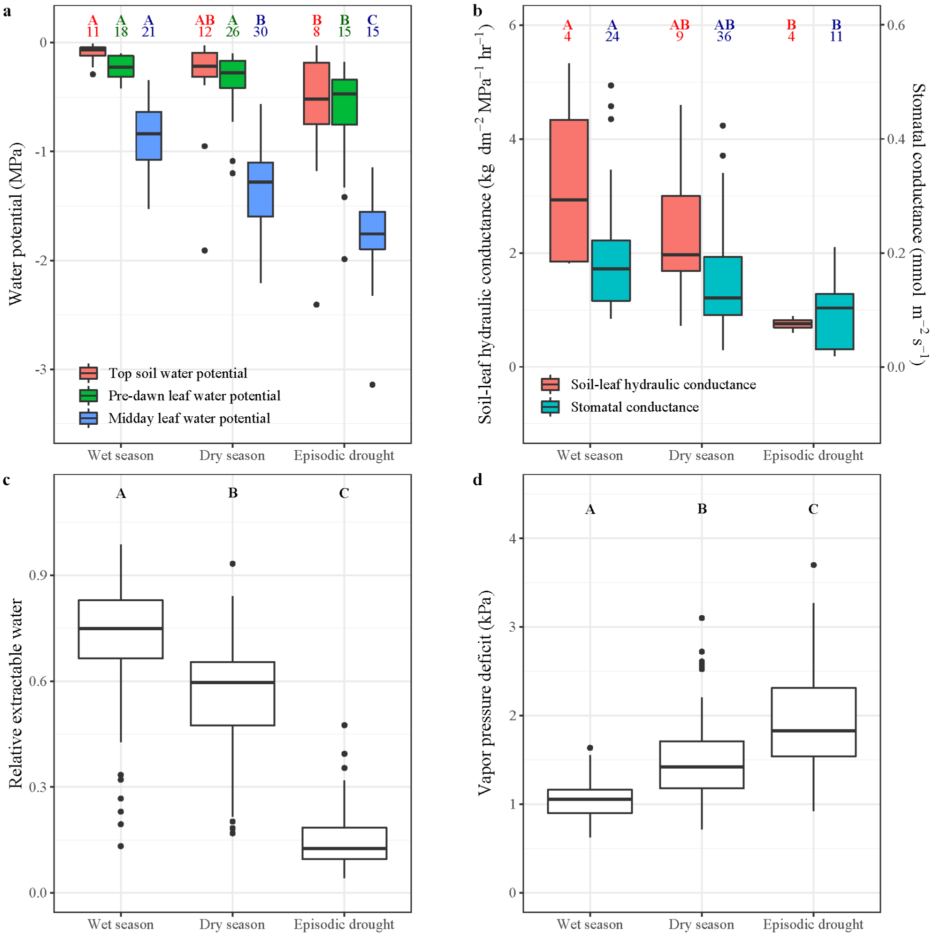
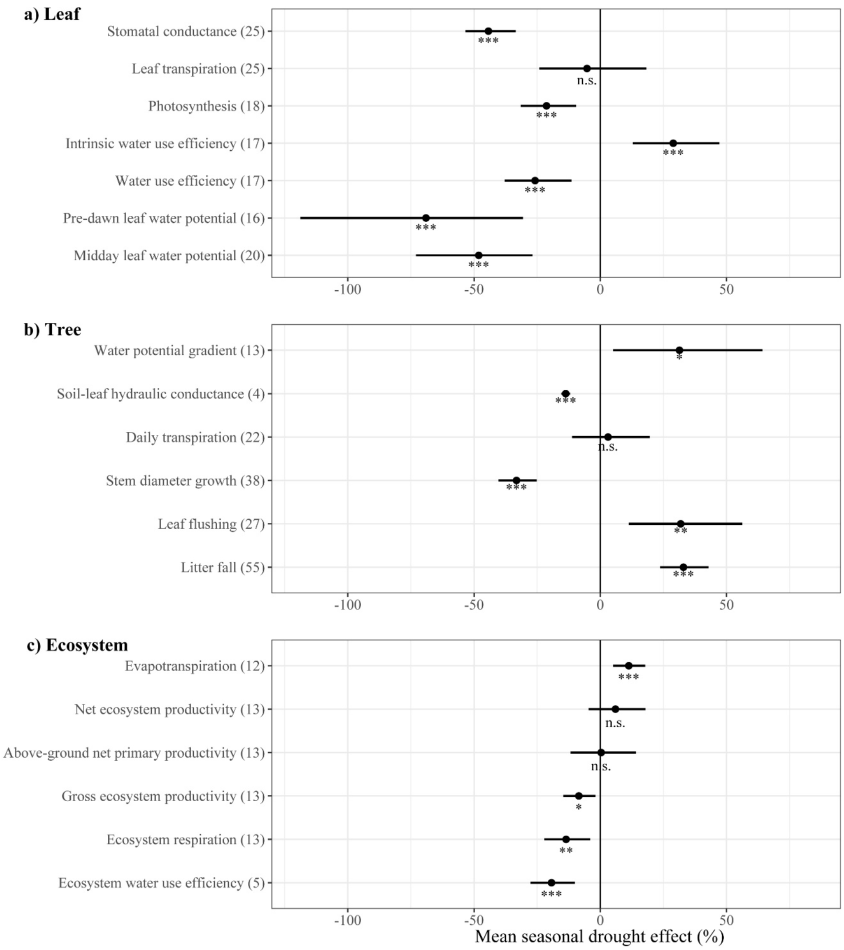


Figure 2: Plant hydraulic status, plant hydraulic conductance, stomatal conductance and environmental drivers in the wet season, dry season and during episodic drought. The boxplots show the median value, interquartile ranges (boxes), the whiskers show the range between minimum and maximum value and, if present, outliers are indicates as single dots. Soil water potential, pre-dawn leaf water potential, midday leaf water potential (a), soil to leaf hydraulic conductance and stomatal conductance (b) are derived from published data and available in the supplementary database. Relative extractable water (c) and vapor pressure deficit (d) are derived from monthly ECMWF ERA5 reanalysis data extracted to 229 neotropical forest sites in South and Central America (1979-2019). Capital letters indicate a significant ($p < 0.05$, Tukey HSD) pairwise difference between the wet season, dry season and episodic

drought values. When a group is not significantly different from the two other groups that are significantly different in the comparison, the capital letters are coupled.


a) Leaf
Stomatal conductance (25) ***
Leaf transpiration (25) n.s.
Photosynthesis (18) ***
Intrinsic water use efficiency (17) ***
Water use efficiency (17) ***
Pre-dawn leaf water potential (16) ***
Midday leaf water potential (20) ***
-100
-50
0
50
b) Tree
Water potential gradient (13) *
Soil-leaf hydraulic conductance (4) ***
Daily transpiration (22) n.s.
Stem diameter growth (38) ***
Leaf flushing (27) **
Litter fall (55) ***
-100
-50
0
50
c) Ecosystem
Evapotranspiration (12) ***
Net ecosystem productivity (13) n.s.
Above-ground net primary productivity (13) n.s.
Gross ecosystem productivity (13) *
Ecosystem respiration (13) **
Ecosystem water use efficiency (5) ***
-100
-50
0
50
Mean seasonal drought effect (%)

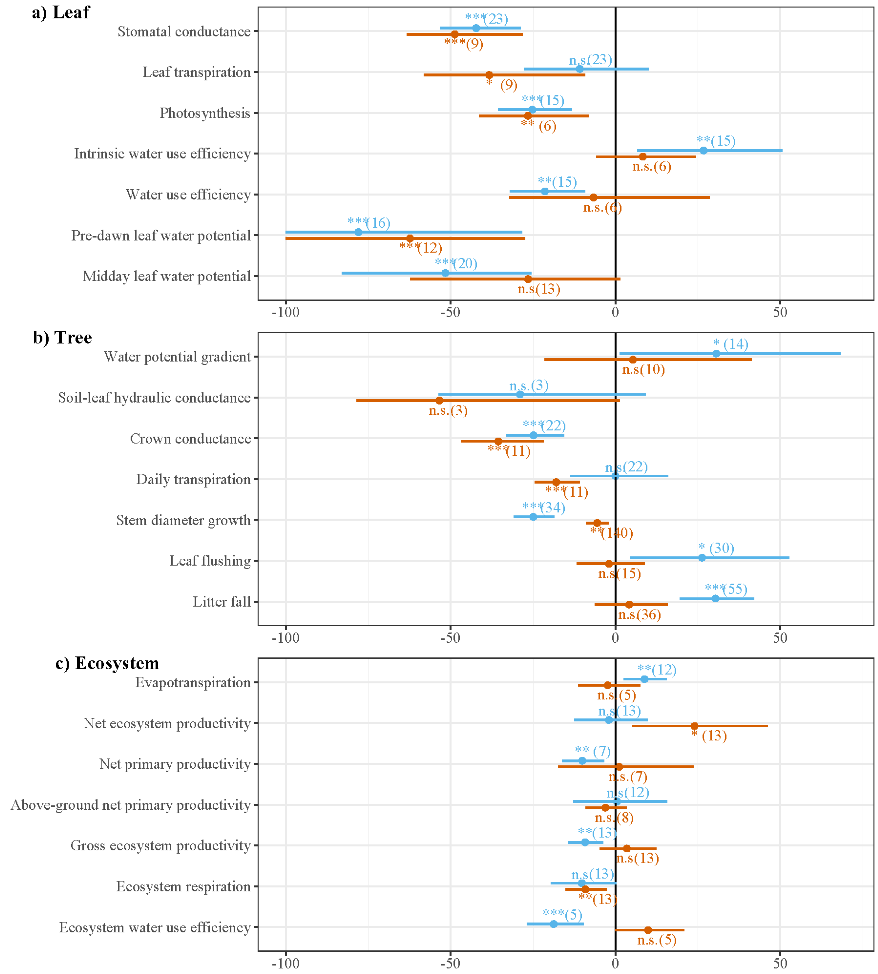
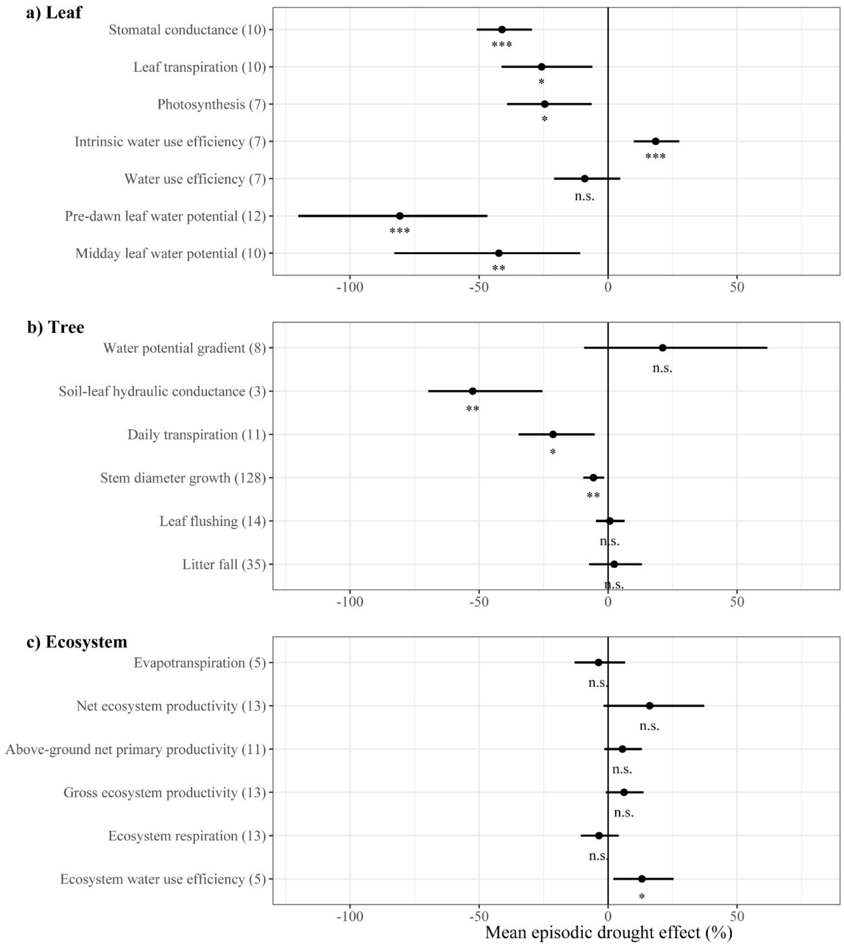


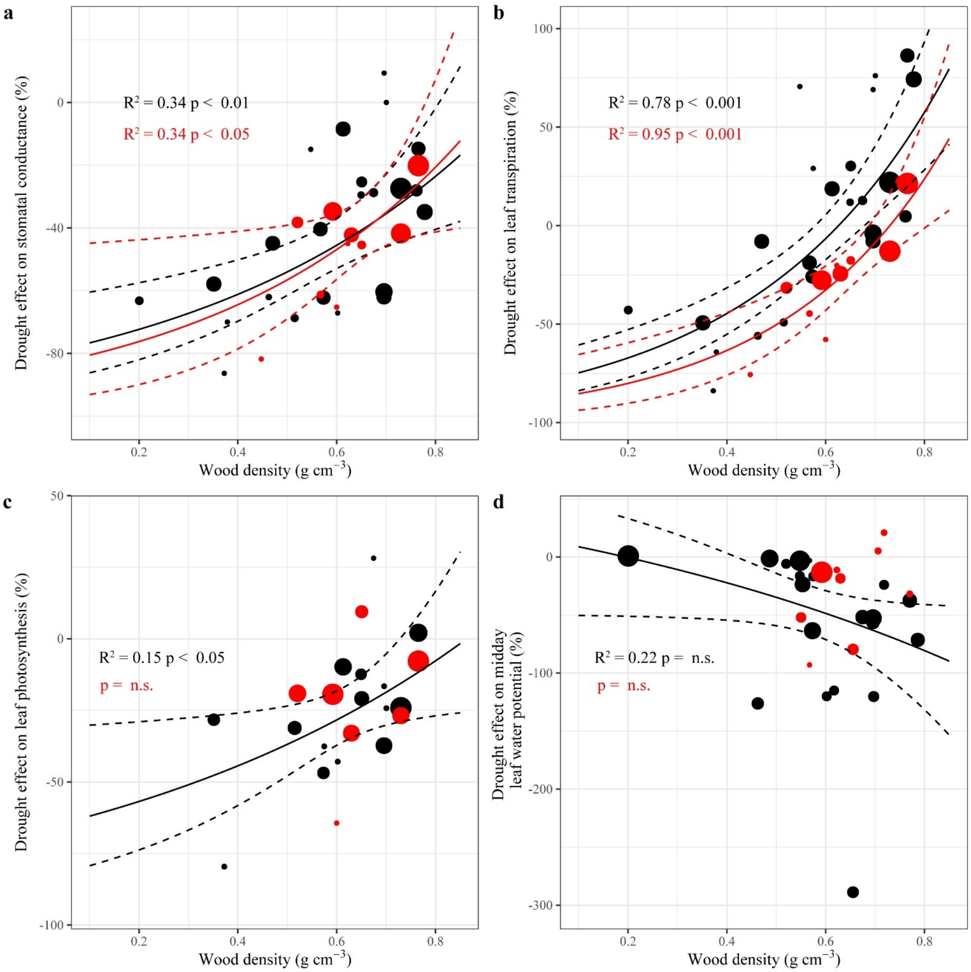
Figure 3: Meta-analysis results of leaf, tree and ecosystem scale responses to seasonal and episodic drought. The ~~values~~ dots are the averages and the horizontal lines represent 95% confidence intervals of percentage change in leaf, tree and ecosystem scale performance ~~from the wet to the dry season~~. The confidence intervals for pre-dawn leaf water potential were cut off at -100% to prevent the x axis from inflating. Repeated measurements were used, therefore the variance of the response ratio is adjusted for by the correlation coefficient between the repeated measurements (Lajeunesse, 2011). The number of consulted studies or sites is

provided in brackets. The significance symbols depict the p-value derived from a Random-effects model (* $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) testing whether the effect size differs significantly from 0.**



~~Figure 4. Meta-analysis results of leaf, tree and ecosystem scale responses to episodic drought. The values are averages and 95% confidence intervals of percentage change in leaf, tree and ecosystem scale performance during episodic drought, relative to an average dry season. Repeated measurements were used, therefore the variance of the response ratio is adjusted for by the correlation~~

~~coefficient between the repeated measurements (Lajeunesse, 2011). The number of consulted studies or sites is provided in brackets. The significance symbols depict the p-value derived from a Random-effects model (*** p < 0.001, ** p < 0.01, * p < 0.05) testing whether the effect size differs significantly~~


a
Drought effect on stomatal conductance (%)
R² = 0.34 p < 0.01
R² = 0.34 p < 0.05
0
-40
-80
0.2
0.4
0.6
0.8
Wood density (g cm⁻³)
b
Drought effect on leaf transpiration (%)
R² = 0.78 p < 0.001
R² = 0.95 p < 0.001
100
50
0
-50
-100
Wood density (g cm⁻³)
c
Drought effect on leaf photosynthesis (%)
R² = 0.15 p < 0.05
p = n.s.
50
0
-50
-100
Wood density (g cm⁻³)
d
Drought effect on midday leaf water potential (%)
R² = 0.22 p = n.s.
p = n.s.
0
-100
-200
-300
Wood density (g cm⁻³)

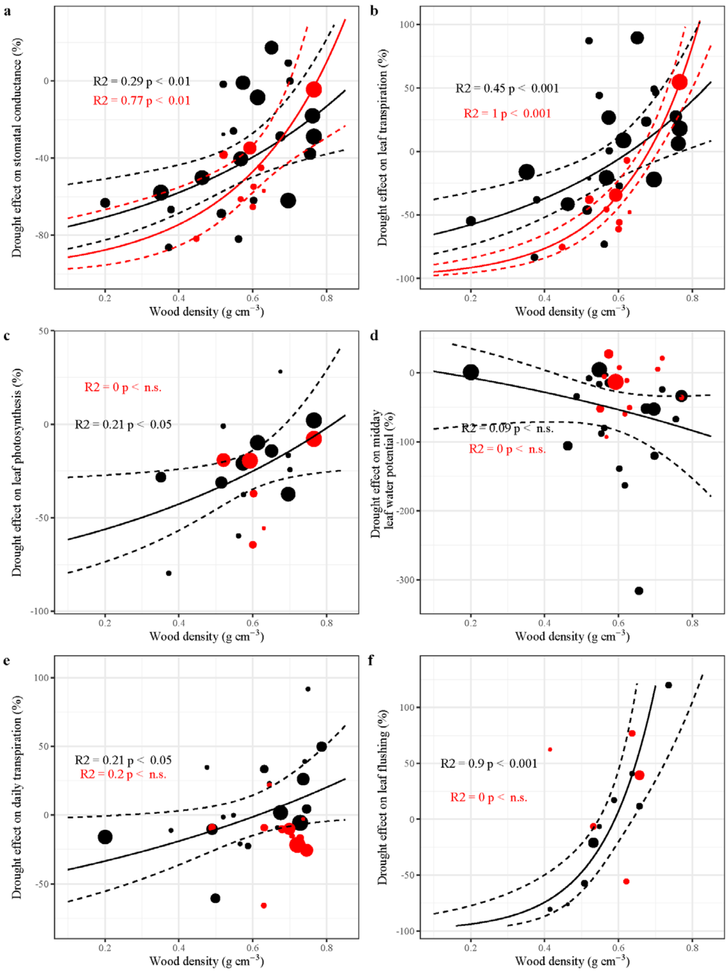
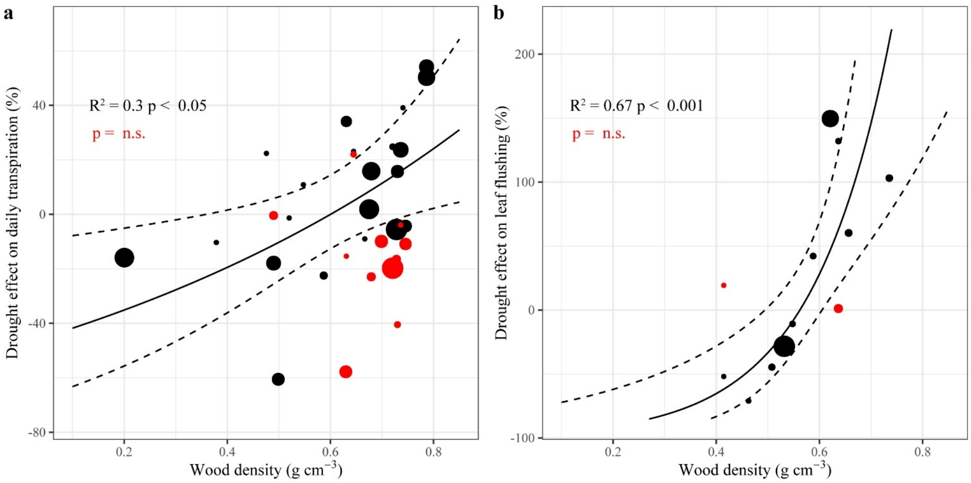


Figure ~~5~~4: Effect size of leaf and tree- scale responses to seasonal drought (black) and episodic drought (red) for different studies against the study averaged wood density. On the leaf-scale, studies with a low average wood density show a decline in stomatal conductance (a), transpiration (b) and photosynthesis (c) in response to seasonal and episodic drought, while midday leaf water potential is not changed. On the tree scale, studies with a low average wood density show a decline in transpiration (e) and leaf flushing (f) to seasonal drought, but not episodic drought. The size of the points is determined based on the inverse of the sampling variance of the particular study (i.e. precision), showing larger points for more precise studies. The sampling variances are used to provide weights to the different studies in the Mixed-effect model. ~~The point size is the inverse of the sample standard error of the~~

~~effect size in the study.~~ The test statistics are retrieved from a Mixed-effect model testing the significance of wood density as a moderator variable in the drought response. The solid line is the model prediction and the dashed lines are the 95% confidence intervals. Regression lines were only drawn if the relationship was significant ($p < 0.05$).



~~Figure 6 Effect size of daily transpiration (a) and leaf flushing (b) to seasonal drought (black) and episodic drought (red) for different studies against the study averaged wood density. The point size is the inverse of the sample standard error of the effect size in the study. The test statistics are retrieved from a Mixed-effect model testing the significance of wood density as a moderator in the drought response. The solid line is the model prediction and the dashed lines are the 95% confidence intervals. Regression lines were only drawn if the relationship was significant (p < 0.05).~~

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