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Dear Nicolas Delbart,

Firstly we would like to thank you for taking the time to review this manuscript. The comments you provided on our manuscript have been very insightful and we believe they have contributed substantially to improving the quality of this manuscript.

In the following pages we provide responses to the comments made on the manuscript. We hope that our responses have dealt with all the issues raised in the review process, however please do not hesitate to contact us if you require any further clarification.

Yours sincerely,

Dr. Lucy Rowland and co-authors.

Response to major and minor comments from reviewer Nicolas Delbart.

(Please note that responses by the authors are shown in red and that our page numbers references are from the revised MS word document)

Major comments:

1. My main comment is about the experimental setup. To my understanding all these models, maybe except ED2, are steady state equilibrium models. However, the experiments carried out in this manuscript consist in rising temperature dramatically and abruptly, or dropping the precipitation, after the model spin-up. Then the model is run for eight years. I am not a model expert but it seems to me these models are not designed to be able to respond adequately in a short term to such disturbances. Thus I am afraid that the model outputs that are presented only reflect how a model adjusts itself during a transition period to a new and totally different climatic situation. I think the models are here used outside of what they are built to do. I think it would be more adequate to impose a temperature increase ramp after the spin-up, or at least run the models much longer than eight years. Moreover that may be more informative on real ecosystem response as it would be closer to realistic climatic changes that do not consist in such abrupt changes. I am not saying the authors should redo the experiments but they must explain very precisely why steady-state equilibrium models can be used in such a way.

We agree that many of these models are designed to only be run in steady state equilibrium conditions. The methodology used for the spin up and model simulations was pre-constrained by a method which tested the capacity to simulate the responses of two experimental drought (see Powell et al 2013), where the forest was indeed exposed to an abrupt change in precipitation, in the model and in the field-scale experiments from which the test data were derived. Working within the existing simulation framework of our modelling consortium our study therefore focuses on model responses to short term shifts in temperature and precipitation at a tropical forest site. We agree that it would be interesting to study a slow ramp-up in temperature as well as a more abrupt change as modelled here. However, we note that there is increasing evidence that this region will experience increasingly severe short-term changes in climate (Cox et al., 2008; Reichstein et al., 2013), and that the Amazon region has already experienced two abrupt and severe drought events in the last decade (Marengo et al., 2011). Hence, whilst testing against a slow ramp up is of much interest, we do still believe that there is significant value in analysing these short-term responses.

Secondly analysing short-term responses is also important as much of the physiology has a fast response timescale, even if (much less well understood) components such as allocation and acclimation may operate over longer timescales. Many of the rapid physiological response mechanisms are dependent on temperature response functions; examples of these which are a key focus of our paper are photosynthetic responses or shifts in VPD which change stomatal conductance (see Figure 1). If we studied these processes after running the models to equilibrium, the responses of some of the key variables in the study (A_n, g_s) are more likely to be dominated by the effect of long term soil drying rather than any direct temperature responses, particularly at the highest temperature changes in the models which simulate a soil water stress function. We acknowledge and discuss in the paper that even at our shorter time-scale the model responses are bound up into responses of the change in soil moisture stress (Lines 383-395), however within the shorter-term time-scales used we argue there is greater scope to look at the shorter-term responses to changes in temperature.

Thirdly because of the responses to variables such as the soil water stress function, if run to equilibrium with the temperature scenarios imposed, many of these models would have shifted from a tropical forest ecosystem to grassland, as CLM3.5 did even over a short time-scale. As discussed below (comment 3) these responses are indeed interesting, but unfortunately not the focus of this paper.

Fourthly analysing data from short-term model simulations allowed us to compare model outputs with the Doughty and Goulden data which looked at short-term instantaneous responses of leaves to increased temperature; this validation/test is particularly valuable because there are very few other datasets beyond Doughty and Goublden focusing on this key issue.

For these reasons above we would argue that this and other studies (e.g. Luo et al., 2008) which explore the short -term responses of Amazonian forest to changes in climate are extremely valuable. However, we agree with the reviewer that we have not made these arguments clear enough in the manuscript and have endeavored to insert the sentences below to amend this:

Lines 31-35: *However, significant uncertainty remains regarding the response of tropical forests to warming (Corlett, 2011; Reed et al., 2012; Wood et al., 2012), altered precipitation (Meir et al., 2008; Meir and Woodward, 2010) and short-term abrupt changes in in both precipitation and temperature (Cox et al., 2008).*

Lines 44-48: *However model responses to simultaneous changes in precipitation and temperature complex are difficult to evaluate due to the compound effect of drought and temperature responses (Luo et al., 2008). There are particular challenges when considering short-to-medium term responses (Luo et al., 2008) linked to climatic extremes, such as severe drought (Cox et al., 2008; Marengo et al., 2011).*

Lines 87-93: *Our model simulations represent short-term non-equilibrium responses to changes in temperature to make them comparable to the perturbation data collected by Doughty and Goulden (2008). Evaluation of non-equilibrium changes in models is valuable for assessing how models will perform when simulating responses to extreme shifts in temperature and precipitation, which are predicted to increase in frequency and severity across Amazonia (Cox et al., 2008; Marengo et al., 2011). If the models were run to their equilibrium response to a simulated climate shift, the changes in some of the key variables in* *the study (A_n, g_s) are more likely to be dominated by the effect of long term soil drying rather than direct temperature responses.*

Lines 351-354: *Had the models been run to their equilibrium states, it is likely that there would have been greater divergence of model responses at both the canopy- and leaf-scales. Prolonged higher temperatures reduce long-term soil moisture availability and cause more severe changes in β; in dynamic-PFT models this can result in a substantial shift of PFT away from tropical forest.*

2. My second comment concerns the conclusions that the authors should give. If it is found that the models only really agree on NEP, less on GPP, and disagree on all processes, it is probably necessary to conclude that despite their complexity these models do not present a clear advantage over simpler models such as light use models or statistical models adjusted on existing ecosystem exchange measurements. Complex models are useful if they allow understanding the mechanisms behind canopy scale measurements, but here we see the models do not bring this knowledge. Thus, the authors should bring a general conclusion on the utility of complex models at their current stage of development to address the question of changes in Amazonian forests in response to climatic variability.

Thank you for raising this point; it is very interesting and something which should be discussed in the manuscript. Model development often advances by using different approaches – simpler (statistical or optimized) and complex. Development of more mechanistic processes should ultimately lead to improvements in our ability to simulate and understand these complex natural systems. We acknowledge that mechanistic understanding is always limited, hence it is certainly very interesting to test if statistical models or simplified 'optimised' models, which may have greater random, but less systematic error, will give a more informative prediction than detailed complex models. This discussion is relevant to many aspects of gross ecosystem process simulation. We hope that we have adequately addressed this issue by introducing a sentence in line 436-442 of the discussion which states:

"The range of model responses in this study is likely to stem from real uncertainty in our understanding of the responses by tropical rain forest ecosystems to changes in precipitation and temperature. Further analysis of the same questions using models that vary in complexity (eg, statistical or optimized models, as well as purely mechanistic) might provide additional insight into mechanistic and simulation bias (systematic or random), as well advancing understanding about climate risk that we derive from them (Meir, Mencuccini and Dewar, 2015)

3. My third comment is that it seems to me that ecosystem response to such large changes (+6◦C) should be treated with the scope of plant functional type changes, as a transition from

forest to savannah should be expected. Except on page 7834 line 12 this crucial question is not addressed, and must be developed.

We agree that the potential transitions from forest to grassland are very important, especially in the context of making ecosystem scale predictions. However there are other manuscripts currently in prep from the same modelling consortium which will discuss the implications of PFT shifts in model simulations done across the Amazon. The focus of this paper was assessing the effects of climate extremes on physiology in tropical forests, particularly in relation to the data comparison aspect of the manuscript. Therefore we did not address the issue of long-term adaptation and forest transitions, as this involves assessment of the competition matrix within the models, which would introduce a new and complex topic into an already complex and fairly long paper. Finally two of the models used in this study do not have multiple PFT's and comparing the responses of these models, to models which do have competing PFT's becomes impossible if PFT shifts occur.

4. My final general comment is about the simulation of respiration. As the inter-model agreement is higher on NEP than on GPP, it is necessary to develop the changes on respiration, and maybe to separate heterotrophic and autotrophic respiration responses. It is commented but not shown, and maybe this is a good option to keep the manuscript in a reasonable length but still these results should be a bit more developed. We also need to know how the models differ in term of both respiration fluxes right after spin-up, and thus the biomass and the soil carbon should also be given to understand the initial differences between the different model simulations.

We agree that the responses of autotrophic and heterotrophic respiration are both very important and that a single graph of total respiration is insufficient to deal with the complexities of this problem. However, the purpose of the respiration figure is not to provide an answer to the responses of respiration fluxes to temperature and drought, but to show the other half of the NEE flux, so the reader can understand what proportion of the NEE response is driven by GPP versus respiration. Although we would be keen to explore the complexities of respiration in detail, this paper is necessarily focused on the gross primary productivity response to climate extremes. Respiration responses are beyond the scope of our paper, which is already relatively complex in addressing leaf to canopy assimilation processes.

In terms of how carbon stocks and fluxes differ between models at this site following spin up, when no climate changes have been imposed, and after drought is imposed, this has already been addressed and published by Powell et al. (2013).

Minor comments:

- Page 7825 Lines 8-10 and 16-18 comment results on GPP and should be grouped. Thank you for pointing this out, now grouped.
- 21 : maybe remove “to” Done
- 23-26: this a key issue. As said page 7837, lines 23-25, uncertainties on LAI are compensated by uncertainties on leaf scale processes. May it be possible that this is explained by the fact that the main source of validation data is canopy scale exchanges measurements? Moreover you point the lack of data later (page 7827), thus which validation strategy are you suggesting here? Thank you for your comment, we have changed the sentence to make it clear that it is validation at both the leaf and canopy scale which is necessary:
  “To improve the reliability of simulations of the response of Amazonian rainforest to climate change the mechanistic underpinnings of vegetation models need to be validated at both leaf- and canopy-scales to improve accuracy and consistency in the quantification of processes within and across an ecosystem. .
- Page 7826, line 23. Meaning of SWC should be given first. Thank you, now done
- Page 7829 lines 14 and 19: same information, should be reorganized. Now re-organised so similar sentences are concatenated
- Page 7834, figure 3. It would be cleared to me to see the LAI changes expressed in LAI units rather than in initial LAI fraction. Moreover, in figure 3, what is shown is not the fraction of change but the fraction that does not change, or am I wrong? Thank you for this comment, we agree that the way we have described the fractional changes in the figure legend is maybe confusing and therefore we have changed the figure legend to read:
  “Figure 3: Modelled effect of short-term changes in temperature and drought. Changes in: a) gross primary productivity (GPP) b) ecosystem respiration (Reco) and c) leaf area index (LAI) in the final year (2006) in the drought run expressed as a fraction of the value in the final year (2006) of the control run, for the Tair -5˚C (grey bars) and Tair +6˚C (White bars) simulations.”
  However, if we were to express LAI in the same figure as LAI units this would be misleading because of the large variation in LAI across the models. For example, if the absolute reductions in LAI from ED2 and CLM3.5 are equivalent in the figure (e.g. they both loose 2$m^2 m^{-2}$ of LAI), the implications are very different. ED2 has a starting LAI of 4 $m^2 m^{-2}$ and thus predicts a 50% loss. Meanwhile, CLM3.5 starts at 11 $m^2 m^{-2}$ and predicts an 18% loss. We believe that the reader therefore gets more information from seeing LAI as a fraction after having already seen the values of LAI between the models in Figure 2.
- Page 7835 : the text here is very complicated, whereas the figure 4 that it described is very clear. I think the manuscript would gain in clarity if the results were described less intensively. Same comment applies elsewhere in the manuscript. We agree that this section

and other results sections were unclear; we have completely re-written the results sections in an attempt to simplify them and make them clearer.

- Page 7837 (lines 1-5) and figure 8: why only two models are shown? As stated in the Methods the data from Doughty and Goulden is only available for sunlit leaves and SPA and CLM3.5 are the only models which simulate an output for sunlit leaves. We have attempted to make this clearer in the Figure legend and in the text in lines 317-319 stating: *"When the effect of soil water stress is removed and sunlit leaf level values are compared to the DG data for the models which could output separate sunlit leaf values of* g_s *and* A_n *(only SPA and CLM3.5; Figure 8)."*

- Figure 1: unclear. What mean signs + and - ? Is it the response of models? Why temperature increase induces an increase in GPP whereas in figure 2 we see the contrary? The + and – signs represent the correlation or possible feedbacks between variables. For example A_n is only positively correlated with GPP, it has a +, (i.e. if An goes up GPP cannot go down, with all other things being equal). Some variable can have both positive and negative feedbacks depending on the magnitude of the change and hence they have both a +/- sign. We have now made this clearer in the legend:
  "Figure 1: Schematic diagram showing how droughts, via the combined effects of increased air temperature (T) and reductions in precipitation (PPT), affect the carbon cycle of a tropical forest, including the effects on: vapour pressure deficit (VPD), evapo-transpiration (E_t)*, stomatal conductance* (g_s)*, soil water content (SWC), net photosynthesis* (A_n)*, leaf area index (LAI), the maximum rates of RuBP carboxylation and electron transport (Vcmax and Jmax respectively), autotrophic respiration* (R_a) *heterotrophic respiration (Rh), gross primary productivity (GPP), and net ecosystem exchange (NEE). + signs indicates a positive feedback effect between variables (i.e. an increase in one variable can only cause an increase in another if all else is equal), - signs indicate a negative feedback effect, and +/- indicate the possibility of both a positive and negative effect. Solid arrows represent responses which occur over short timescales of minutes to hours, whereas dashes arrows represent responses which can occur over longer timescales from days to months."*

- Figure 5: should be expressed in the units of Vcmax, not relatively to 25◦C. The key point of Figure 5 within our paper is to show the relative responses of V_{cmax} to temperature change. We argue that this is much easier to see if you explore the shapes of the temperature response curves on a normalised scale, where the response curve can be directly compared across models. Within the models V_{cmax} is the only variable explored which has a fixed temperature response independent of other climate variations, for example VPD. If we were to plot the actual values the resulting figure would be very confusing because some of the models output V_{cmax} values for the top canopy only, before canopy integration occurs, and other models output an integration of V_{cmax} across the canopy, or different V_{cmax} values from multiple canopy levels. Consequently the absolute values for V_{cmax} across the models are not comparable whereas the temperature responses on V_{cmax} are. If necessary we can clarify this point in the Figure legend.

- Table 3, caption : unclear. This caption has now been re-written, to what we hope is a much clearer format:
  "Table 3: Values show the normalised intrinsic water use efficiency (IWUE) calculated as the linear slope of normalised A_n plotted against normalised g_s (Figure 6). The normalised IWUE is calculated separately for each models' control and drought temperature simulations (ambient air temperature (T_{air}) -5˚C, +0 ˚C,+2 ˚C,+4 ˚C, and +6 ˚C)."

- I apologize but interpretation of figures 6 and 7 are unclear to me. Thank you for pointing out that the interpretation of Figures 6 and 7 are not 100% clear. The purpose of Figures 6 and 7 is: firstly to demonstrate that there are clear relationships between A_n and g_s in the models, but not between A_n and V_{cmax}. We hope that this is now clearer in lines 299-301: "*Consequently for each model there are apparent, but variable, relationships between gs and An (Figure 6), but no obvious relationships between An and Vcmax (Figure 7).*"
  Figure 6 is also used to show the normalised intrinsic water use efficiency: the normalised increase in A_n per unit increase in normalised g_s. The purpose of this plot is to show that the rate at which normalised A_n increases per unit increase in normalised g_s (i.e. the linear slope) increases from the lowest temperature simulation (ambient air temperature -5˚C) to the highest temperature simulation (ambient air temperature +6˚C) and this increase is greater in the drought than control simulations. The normalised values of intrinsic water use efficiency per simulation (the linear slope values) are shown in Table 3
  The results and discussion sections in this manuscript which include the explanation of the results from these figures have now all been re-written (see comment above), as have the figure captions. We hope now that the figures and results concerning these figures are now made much clearer throughout the manuscript.

New references added to text and manuscript:

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3. Gatti, L. V., Gloor, M., Miller, J. B., Doughty, C. E., Malhi, Y., Domingues, L. G., Basso, L. S., Martinewski, A., Correia, C. S. C., Borges, V. F., Freitas, S., Braz, R., Anderson, L. O., Rocha, H., Grace, J., Phillips, O. L., and Lloyd, J.: Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements, Nature, 506, 76, 2014. doi:10.1038/Nature12957
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5. Meir, P., Mencuccini. M., and Dewer. R. C. Tree mortality during drought: narrowing the gaps in understanding and prediction, New Phytologist, in press.
6. Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., Wattenbach, M. (2013) Climate extremes and the carbon cycle. Nature 500, 287-295. doi 10.1038/Nature12350.

Modelling climate change responses in tropical forests: similar productivity estimates across five models, but different mechanisms and responses.

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Abstract

Accurately predicting the response of Amazonia to climate change is important~~important~~ for predicting climate change~~s~~ across the globe. ~~However, changes~~ Changes in multiple climatic factors simultaneously ~~may~~ result in complex non-linear ecosystem responses, which are difficult to predict using vegetation models. Using leaf- and canopy-~~-~~scale observations, this study evaluated the capability of five vegetation models (CLM3.5, ED2, JULES, SiB3, and SPA) to simulate the responses of ~~canopy~~leaf- and ~~leaf-~~ canopy-scale productivity to changes in temperature and drought in an Amazonian forest.

The models did not agree as to whether gross primary productivity (GPP) was more sensitive to changes in temperature or precipitation, but all the models ~~did~~were consistent with the prediction~~ed~~ that GPP would be higher if tropical forests were 5°C cooler than current ambient temperatures.~~.~~ There was greater model-data consistency in the response of net ecosystem exchange (NEE) to changes in temperature~~,~~ than in the response to temperature ~~of~~ by ~~leaf area index (LAI),~~ net photosynthesis (A_n), ~~and~~ stomatal conductance (g_s) and leaf area index (LAI) ~~stomatal conductance (g_s)~~. Modelled canopy-~~-~~scale fluxes are calculated by scaling leaf-~~-~~scale fluxes ~~to~~ using LAI~~,~~.~~and therefore i~~ At the leaf-scale, the models did not agree on the temperature or magnitude of the optimum points of A_n, V_{cmax} or g_s~~-~~, and model variation in these parameters ~~were~~ was compensated for by variations in the absolute magnitude of simulated LAI, and how it altered with temperature. ~~and temperature response of LAI~~

~~n this study similarities in modelled ecosystem scale responses to drought and temperature were the result of inconsistent leaf scale and LAI responses among models.~~

~~A~~Across the models, there was, however, consistency in two leaf-scale ~~the~~ responses: 1) ~~of~~ change~~s~~ in A_n ~~to~~ with temperature were~~as~~ more closely linked to stomatal behaviour than

biochemical processes; and 2) intrinsic water use efficiency increased with temperature, especially ~~with simultaneous~~ when combined with drought. These results suggest that even up to fairly extreme temperature increases from ambient levels (+6˚C), simulated photosynthesis becomes increasingly sensitive to g_s and remains less sensitive to biochemical changes.~~. Consequently all the models predicted that GPP would be higher if tropical forests were 5°C colder, closer to the model optima for g_s. There was however no model consistency in the response of the A_n-g_s relationship when temperature changes and drought were introduced simultaneously. The inconsistencies in the A_n-g_s relationships amongst models were caused by to non-linear model responses induced by simultaneous drought and temperature change.~~ To improve the reliability of simulations of the response of Amazonian rainforest to climate change, the mechanistic underpinnings of vegetation models need ~~more complete validation~~to be validated at ~~the scales of~~both ~~the~~ leaf- and canopy-scales to improve accuracy and consistency in the ~~scaling~~ quantification of ~~ecosystem~~ processes within and across an ecosystem.~~ from leaf to canopy.~~

1 Introduction

Continuing increases in atmospheric CO_2 are likely to cause increases in temperature and changes in precipitation across Amazonia (Good et al., 2013; Jupp et al., 2010; Malhi et al., 2009; Marengo et al., 2012). However, significant uncertainty remains regarding the response of tropical forests to warming ~~temperatures~~ (Corlett, 2011; Reed et al., 2012; Wood et al., 2012), ~~and~~ altered precipitation (Meir et al., 2008; Meir and Woodward, 2010) and short-term abrupt changes in both precipitation and temperature (Cox et al., 2008; Marengo et al., 2011; Reichstein et al., 2013). Such uncertainties are propagated into models, resulting in substantial variability in modelled responses to changes in temperature and drought (Friedlingstein et al., 2006; Galbraith et al., 2010; Powell et al., 2013; Sitch et al., 2008). These responses need to be rigorously assessed to enable further improvement in our ~~current cap~~ability to predict the impacts of climate change on rain forest functioning.

The ecosystem responses of models to multi-factor changes in climate can be difficult to interpret because of complex nonlinear responses (Zhou et al., 2008), which can vary substantially between vegetation models with different model structures. Previous modelling analyses have shown a greater sensitivity of carbon storage in Amazonian forests to increased temperature than reduced precipitation (Galbraith et al., 2010). However ~~the compound effect of drought on temperature responses when simulating Amazonian forest processes (Luo et al., 2008), makes evaluating model~~ model responses to simultaneous changes in precipitation and temperature complex are difficult to evaluate due to the compound effect of drought and temperature responses (Luo et al., 2008). There are particular challenges when considering ~~the~~ short-to-medium term responses (Luo et al., 2008) linked to climatic extremes, such as severe drought (Cox et al., 2008; Marengo et al., 2011).~~.~~

Concurrent changes in temperature and precipitation can cause a complex chain of positive and negative feedbacks on different timescales (Figure 1). Increased temperature and reduced precipitation can directly affect stomatal conductance (g_s) through increasing vapour pressure deficit (VPD), or indirectly affect~~ing~~ g_s on longer time-scales through reducing soil water content (SWC; ~~(~~Figure 1). Stomatal conductance, ~~g_s~~ g_s, limits photosynthesis (A_n), and therefore gross primary productivity (GPP). However A_n can also be limited by changes in leaf biochemistry (V_{cmax} and J_{max}, Figure 1). How A_n is limited by temperature increase is important as changes in leaf biochemistry at very high temperatures ~~are the~~ can result ~~of~~ from permanent alteration and possible damage to proteins, whereas changes in g_s are less permanent, but ~~result in changes in~~ alter water use, and potentially water use efficiency. Currently there is no consensus on how A_n will respond to temperature~~,~~: some studies find a direct impact through leaf biochemistry (Doughty, 2011; Doughty and Goulden, 2008), and others an indirect effect initiated by changes in g_s, because ~~of~~the limitation of increasing VPD on g_s ~~limitation occurring~~ occurs at lower temperatures than those ~~required~~ that cause ~~for~~ protein damage (Lloyd and Farquhar, 2008). The lack of data for tropical trees means these responses remain poorly constrained, though drought and warming can be examined using limited field data from drought and warming experiments (da Costa et al., 2014; da Costa et al. 2010~~3~~; Nepstad et al., 2002) and from extreme events within the natural range of the climate (Marengo et al., 2012).

The response of vegetation models to temperature change or drought occurs through the aggregated changes in finer scale processes, for example at the leaf level. Correctly simulating the mechanisms at the leaf ~~-~~scale is therefore important to maintain confidence in canopy-scale predictions. Leaf-scale responses in models are scaled using LAI to simulate the processes at ~~the scale of~~ the ~~canopy scale~~canopy-scale~~,~~~~scale~~; therefore inaccuracies in ~~both leaf scale fluxes or~~both leaf-scale fluxes and how they are scaled can produce substantial errors in ecosystem scale fluxes (Bonan et al., 2012). Currently no model-data comparisons exist that allow for the evaluation of combined temperature and precipitation/drought sensitivity of ecosystem fluxes in relation to LAI and ~~leaf scale~~leaf-scale processes in tropical forests. However if we are to identify accurately how to improve simulated responses of Amazonian forests to future climate change it is vital that model output is evaluated against data from the leaf to the ~~canopy scale~~canopy-scale .

At the Tapajós national forest in north east Brazil, Doughty and Goulden (2008) collected data on the response of net ecosystem exchange (NEE) to change in atmospheric temperature and the response of A_n and g_s to short-term artificial leaf warming. Doughty and Goulden (2008) found reductions in forest productivity at air temperatures above 28˚C, which corresponds to significant reductions in A_n and g_s at leaf temperatures above 30-33˚C. They suggested that tropical forests may therefore already be close to a temperature threshold, beyond which productivity will decline.

Here we use the data published by Doughty and Goulden (2008) to evaluate the short-term temperature responses within models at both the leaf and ~~canopy scale~~canopy-scale ~~–~~and investigate how the model formulations might impact predicted responses to multiple climatic factors. Our model simulations represent short-term non-equilibr~~ated~~ ium responses to changes in temperature to make them comparable to the perturbation data collected by

Doughty and Goulden (2008). Evaluation of non-equilibr~~ated~~ium changes in models is valuable for assessing how models will perform when simulating responses to extreme shifts in temperature and precipitation which are predicted to increase across Amazonia (Cox et al., 2008; Marengo et al., 2011). If the models were run their equilibrium response to a simulated climate shift, ~~,~~the changes in some of the key variables in the study (A_n, g_s) are more likely to be dominated by the effect of long-term soil drying rather than direct temperature responses (e.g. the dashed lines in Fig. 1). This study is part of a wider model inter-comparison project which aims to explore how well vegetation models simulate drought in the eastern Amazon (Powell et al., 2013). In this study we evaluate: 1) how the forest productivity of five vegetation models (CLM3.5, ED2, JULES, SiB3, SPA) responds to changes in temperature, 2) what leaf-~~-~~scale processes drive canopy-~~-~~scale changes in productivity and 3) how both leaf- and canopy-~~-~~scale temperature sensitivities are influenced by concurrent changes in precipitation at the Tapajós forest site in eastern Brazil. In all models we simulate first an ambient and then a 50 % reduction in the incoming precipitation during the wet season from 2000-2006 analogous to the ~~imposed~~ drought treatment imposed at the Tapajós forest site, linked to a -5˚C, 0˚C, +2˚C, +4˚C, and +6˚C change to the ambient air temperature (T_{air}). These simulations cover a range of likely and possible increases in temperature for the Amazon region in the coming century (Christensen et al, 2007; Collins et al., 2013; Malhi et al., 2009) and can be evaluated against existing data from Doughty and Goulden (2008). This study is the first to evaluate, using data, the inter-model variability in the leaf and canopy responses to changes in temperature and precipitation at a tropical forest site.

2 Materials and Methods

2.1 Model description

The five models used in this study were the Community Land Model version 3.5 coupled to the Dynamic Global Vegetation model (CLM3.5-DGVM; hereafter CLM3.5), the Ecosystem Demography model version 2 (ED2) , the Joint UK Land Environment Simulator version 2.1 (JULES), the Simple Biosphere model version 3 (SiB3), and the Soil-Plant-Atmosphere model (SPA)~~ and~~.~~ the Joint UK Land Environment Simulator version 2.1 (JULES).~~ A brief description of each of the models is given here and in Table 1 (also see Powell et al., (2013)). The simplest canopy structure is in Si~~I~~B3. ~~SIB3~~ SiB3 has a fixed LAI and uses a big-leaf model which simulates the response of the top canopy and integrates this response throughout the canopy according to a light and leaf nitrogen (N) extinction coefficient (Baker et al., 2008~~b~~; Sellers et al., 1992; Sellers et al., 1996). CLM3.5 is also a big-leaf model, however it separates the canopy into a sunlit leaf fraction (leaves which receive both direct and diffuse light) and a shaded leaf fraction (leaves which receive only diffuse light), which change dynamically with sun angle and canopy light penetration (Oleson et al., 2004; Oleson et al., 2008). The version of JULES used in this study simulates 10 canopy layers with equal leaf area increments. Leaf nitrogen decays exponentially through the canopy and radiation interception is simulated following the two-stream approximation of Sellers (1985). SPA also has a layered canopy model, and here used three canopy layers, with separate sunlit and shaded fractions (Williams, 1996; Williams et al., 2005). ED2 mathematically approximates the properties of an individual-based forest gap model, separately modelling the stems of three successional stages (pioneer, mid-successional and late-successional)~~types~~ of, in this study, tropical trees ~~(early, mid and late successional)~~ and grasses on a continuum of leaf light levels from fully shaded to fully sunlit (Kim et al., 2012; Medvigy et al., 2009b; Moorcroft et al., 2001). ~~SIB3~~ SiB3 and SPA simulate only 1 plant functional type (PFT), set to tropical evergreen broadleaf; JULES and CLM3.5 simulate 5 PFT's, but this site simulated a fractional cover > 95% evergreen broadleaf trees. As the focus of this study is the responses within tropical forests, results were not considered if a model simulated a shift in the PFT away from the dominance of tropical forest. ~~ED2 simulates 3 successional stages (pioneer, mid-successional and late-successional) of a single PFT, tropical evergreen broadleaf trees.~~

All of the models use enzyme-kinetic A_n equations, derived from Farquhar et al. (1980), Farquhar and Sharkey (1982), Kirschbaum and Farquhar (1984) and Collatz et al. (1991). In all models temperature can affect A_n directly through temperature response functions on the maximum rate of carboxylation of RuBP (V_{cmax}), the CO_2 compensation point, and the Michaelis-Menten constants (K_c and K_o), and in SPA the maximum rate of electron transport (J_{max}). Temperature can also indirectly change A_n through changing the VPD at the leaf surface, which alters g_s. CLM3.5, ED2 and ~~SIB3~~ SiB3 use the Ball-Berry stomatal conductance model (Collatz et al., 1991). JULES calculates g_s by relating the ratio of internal to external CO_2 to the humidity deficit (Cox et al., 1998). SPA is unique in that it models stomatal conductance by simulating an aqueous continuum between the soil and leaf water: g_s and photosynthesis are maximised using an isohydric assumption that at each time-step leaf water potential does not drop below a critical level (-2.5 MPa; see Williams et al., 1996, Fisher et al., 2007). CLM3.5, ED2, ~~SIB3~~ SiB3 and JULES alter g_s using a water stress factor (β; a value ranging 0-1 where 1 indicates no soil water stress and 0 indicates complete soil water limitation). A detailed description of the effect of soil water stress on g_s and A_n in these models is given by Powell et al., (2013).

2.2 Site

The throughfall exclusion in the Tapajós National Forest (TNF, 2.897 S, 54.952 W) is located on an Oxisol soil, and has a mean annual precipitation of approximately 2 m per year; the site is described in detail by Nepstad et al. (2002). This plot was selected for this experiment because on the temperature response of canopy level net ecosystem exchange (NEE) was collected at a nearby site (km83; Doughty and Goulden, 2008). The canopy NEE measurements were from an eddy covariance tower from July 2000 to July 2001, when light levels were above 1000 μmol m^{-2} s^{-1} (Doughty and Goulden, 2008). Leaf level responses of stomata conductance and photosynthesis to increases in leaf temperature in fully sunlit canopy leaves were from 3 species in 2004 (see Doughty and Goulden, 2008 and Goulden et al., 2004).

2.3 Meteorological Data and Soil Properties

The model simulations were driven using hourly meteorological data (precipitation, T_{air}, specific humidity, short and long-wave radiation and air pressure) measured above the canopy at the site from 01/01/2002-31/12/2004. The short-wave radiation was split into 68% direct and 32% diffuse, and then this was split into 43% visible and 57% near-infrared for direct, and 52% visible and 48% near-infrared for diffuse (Goudriaan, 1977).

The soil properties were standardised across all models to create a similar soil physical environment, thereby testing only for differences in vegetation functioning (see Powell et al., 2013). Only biological properties such as rooting depth, root biomass, as well as the total number of soil layers were left as model specific soil properties.

2.4 Experimental design

All of the models went through a standard spin-up procedure prior to simulations (see Powell et al., 2013). Following the spin-up period, a series of five model simulations, with varying T_{air}, were performed for an eight-year period (which was intended to simulate 1999-2006, see Powell et al., 2013) for ambient precipitation (control simulations) and for simulations with a 50 % reduction in wet season rainfall (drought simulations). The 2002-2004 meteorological data were recycled over the eight year simulation period. To explore the effects of changes in T_{air} on the models we performed five model simulations which consisted of simulations with the hourly 2000-2006 ambient T_{air} adjusted by -5˚C, 0 ˚C (ambient T_{air}), +2˚C, +4˚C and +6˚C. 1999 was the baseline year for which no changes from ambient temperature and precipitation were implemented. Our analysis was focused on increases in temperature; however we included a simulation with temperatures 5 ˚C lower than ambient temperatures, on the basis that some models may have processes optimised for temperate regions where average T_{air} is lower. VPD was adjusted according to the changes in air temperature.

2.5 Model output and evaluation

All the data in this study was processed to match the collection methods and processing done by Doughty and Goulden (2008; hereafter referred to as DG), as closely as possible. Therefore, to compare the models' predictions NEE with the flux data, we extract canopy level fluxes when photosynthetic photon flux density (PPFD) was > 1000 µmol m^{-2} s^{-1}, the conditions used by DG. PPFD was not available for the whole period; therefore we use the measured shortwave radiation to estimate PPFD. A conversion factor of 2 is used to convert from shortwave radiation (W m^{-2}) to PPFD (µmol m^{-2} s^{-1}) based on an empirical relationship calculated from the flux tower at the study site (Doughty, unpublished data). The results on hourly time-steps from each model for the period of (2000-2006) for the five ~~ambient~~ temperature simulations (with offset of -5˚C, +0˚C, +2˚C, +4˚C and +6˚C) were pooled. Model output was then placed into 1 ˚C bins of T_{air} for the canopy-scale analysis (GPP, NEE, ecosystem respiration (R_{eco})) or of leaf temperature (T_{leaf}), for ~~leaf scale~~leaf-scale -analysis, as done in the DG study. Accounting for non-gaussian distributions in model output the median and the 15.9th and 84.1th quantiles of the binned model output are plotted to represent the mean and 1 standard deviation of the temperature response curve of any model variable. The data from the drought and control simulations are considered separately.

To explore the relative sensitivity of models to changes in temperature and drought a linear relationship between the temperature increase per control simulation (-5 ˚C, 0 ˚C, 2 ˚C, 4 ˚C, 6 ˚C) and final year (2006) GPP was used to calculate the change in GPP per 1˚C increase T_{air} for each model (Table 2). This value was used to calculate the increase in temperature necessary to produce the same loss of GPP as the ambient T_{air} drought simulation, where there is a 50% reduction in wet season rainfall (Table 2).

DG published data for the temperature response of A_n and g_s of sunlit leaves during the dry season when PPFD is >1000 µmol m^{-2} s^{-1}. CLM3.5 and SPA are the only models which have separate output for sunlit and shaded leaves. Consequently data from the sunlit leaves of these models from periods of high PPFD (>1000 µmol m^{-2} s^{-1}) during the dry season (July-December) were used for comparison. The effect of increasing T_{air} reducing modelled soil water content (via increased VPD and consequent leaf transpiration) had to be removed from the model outputs to make it comparable to the DG data, where individual leaves were artificially warmed. Therefore we only selected model outputs from the temperature simulations if the soil water content in the rooting zone was in the top quartile of the values from the ambient control simulation, this corresponded to β values of >0.9 in CLM3.5. For consistency with the sunlit leaf analysis, the analysis of canopy average leaf data from all models was done using dry season data with PPFD >1000 µmol m^{-2} s^{-1}.

The relative sensitivity of the five models to changes in temperature and precipitation is assessed by comparing the interactive and non-interactive effects of the 50 % reduction in wet season precipitation (drought simulation) with the -5˚C, 0, and +6˚C change in T_{air} on ecosystem fluxes at the end of the 8 year simulation (2006).

3 Results

3.1 ~~Canopy scale~~Canopy-scale responses

The models have similar responses of NEE and GPP to increasing T_{air}. DG observed a reduction in carbon uptake as NEE went from -17.4±0.3 to -7.9±1.1 µmol m^{-2} s^{-1}, corresponding to an increase in T_{air} from 28˚C - 32˚C (Figure 2a). The modelled NEE begins to increase at a lower T_{air} (22-25˚C) in the models and the 28˚C - 32˚C increase in NEE is generally substantially less than observed by DG (2.5-3.9 µmol m^{-2} s^{-1}), except in SPA which experiences a similar increase in NEE as DG from 28˚C - 32˚C (8.8 µmol m^{-2} s^{-1}), across the same range of values (-15.8 to -7.0 µmol m^{-2} s^{-1}; Figure 2a). The increase in modelled NEE at high temperatures is caused by a decline in GPP across all models (Figure 2b). As T_{air} increases from 16˚C to 38˚C the average decline in GPP from all models is 20.9±3.2 µmol m^{-2} s^{-1}. In contrast the mean model decline in R_{eco} over the same modelled T_{air} range was 4.2±1.8 µmol m^{-2} s^{-1} (Figure 2c). The decline in modelled ecosystem respiration is low because in all models a decline in autotrophic respiration with increasing temperature (linked in the models with reduced GPP) is opposed by an increase in heterotrophic respiration (data not shown).

Declines in GPP corresponded to declines in LAI. Between 25˚C to 38˚C the decline in GPP in CLM3.5 (89±38 %), and SPA (82±26 %) was greater than in other models (Figure 2b) and matched by greater declines in LAI over the same temperature range (4.2±1.0 m^2 m^{-2}, CLM3.5 and 4.4±0.9 m^2 m^{-2} in SPA, relative to only 0.6±0.3 m^2 m^{-2} in ED2 and 0.4±0.1 m^2 m^{-2} in JULES; Figure 2d). The inter-model variability in LAI is large; at 25 ˚C the median LAI value in ED2 (3.6±0.3 m^2 m^{-2}) is 3 times smaller than the median values in CLM3.5 (10.7±1.0 m^2 m^{-2}). Observed mean LAI at the TNF under non-drought conditions ranged from 5.5-6.3 m^2 m^{-2} from 2000 to 2005 (Brando et al., 2008) and therefore the modelled values span a range ~70% above and below the measured LAI (Figure 2d).

Combined drought and warming had compound effects on GPP, R_{eco}, and LAI. In CLM3.5

GPP remained the same in the T_{air} -5˚C simulation at the end of the drought and control simulation, however in the T_{air} +6˚C simulation the forest which existed at the end of the control simulation was replaced with grassland in the drought simulation (GPP values for grassland are not shown, Figure 3a). In JULES, SiB3 and SPA the GPP was the same in the control and the drought simulation at T_{air} -5˚C; however GPP is 61%, 58% and 44% lower respectively at the end of the drought relative to the control simulation (Figure 3a). The combined effect of temperature and drought on GPP and R_{eco} is lowest in ED2, because it was the only model to have a strong drought effect on GPP, R_{eco} and LAI in the T_{air} -5˚C simulation (Figure 3). In CLM3.5 and SPA, GPP and LAI have the same fractional reductions with drought, at higher temperatures (Figure 3a and 3c), indicating a tight coupling between the LAI and canopy productivity; this contrasts the lack of, or low GPP-LAI feedback in SiB3 and JULES.

Amongst the models there is a continuum of temperature versus drought sensitivity. We express the temperature versus drought sensitivity as the equivalent temperature increase necessary to produce the same GPP reduction as between the last year of the control to the drought simulation at ambient T_{air} (Table 2). A low equivalent temperature would represent a greater GPP sensitivity to temperature increase and/or a lower GPP sensitivity to drought; a higher equivalent temperature represents a lower GPP sensitivity to temperature increase and/or a higher GPP sensitivity to drought. The equivalent temperature increase necessary to reproduce the same GPP reduction as from the last year of control and droughts simulation at ambient temperature was lowest in SPA (4.92˚C), moderate in JULES and CLM3.5 (8.61˚C and 8.83˚C, respectively), and highest in SiB3 and ED2 (15.70˚C and 17.50˚C, respectively; Table 2). However across all the models a 5˚C reduction in ambient T_{air} resulted in an increase in forest productivity as GPP rose between 3.3-8.7 Mg C ha^{-1} yr^{-1} in all models (Table 2).

~~The models have similar responses of NEE and GPP to increasing T_{air}. DG observed a reduction in carbon uptake as NEE went from -17.4±0.3 to -7.9±1.1 µmol m^{-2} s^{-1}, corresponding to an increase in T_{air} from 28˚C – 32˚C (Figure 2a). The modelled NEE begins to increase at a lower T_{air} (22-25˚C). The modelled increase in NEE from 28˚C – 32˚C, in all models except SPA (2.47-3.87 µmol m^{-2} s^{-1}), is substantially less than observed by DG; model increases in NEE in SPA from 28˚C – 32˚C are closer to those observed by DG (-15.8 to -7.0 µmol m^{-2} s^{-1}; Figure 2a). The increase in modelled NEE at high temperatures is caused by a decline in GPP across all models (Figure 2b). As T_{air} increases from 16˚C to 38˚C the average decline in GPP from all models is 20.9±3.2 µmol m^{-2} s^{-1}. In contrast the mean model decline in R_{eco} over the same modelled T_{air} range was 4.2±1.8 µmol m^{-2} s^{-1} (Figure 2c). The decline in modelled ecosystem respiration is low because in all models a decline in autotrophic respiration with increasing temperature (linked in the models with reduced GPP) is opposed by an increase in heterotrophic respiration (data not shown).~~

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~~from 5.5-6.3 m^2 m^{-2} from 2000 to 2005 (Brando et al., 2008) and therefore the modelled values span a range ~70% above and below the measured LAI (Figure 2d).~~

~~Combined drought and warming had compound effects on GPP, R_{eco}, and LAI. In Figure 3 the change in GPP, R_{eco}, and LAI for the T_{air} -5˚C and T_{air} +6˚C simulations relative to the control simulation in the last year (2006) of the drought simulation is shown as a fraction of the year of the control simulation. The effect of temperature and drought was strongest in CLM3.5 where GPP is the same in the drought and control simulation at T_{air} –5˚C, but where a complete forest dieback to grassland was observed when drought was combined with a +6˚C temperature increase (GPP values for grassland are not shown, Figure 3a). In JULES, SiB3 and SPA the GPP was also the same in the control and the drought simulation at T_{air} –5˚C; however GPP is 61%, 58% and 44% lower respectively than the control when a +6˚C increase in T_{air} occurs simultaneously with drought (Figure 3a). The combined effect of temperature and drought on GPP and R_{eco} is lowest in ED2, because it was the only model to have a strong drought effect on GPP, R_{eco} and LAI in the T_{air} –5˚C simulation (Figure 3). In CLM3.5 and SPA, GPP and LAI have the same fractional reductions with drought, at higher temperatures (Figure 3a and 3c), indicating a tight coupling between the LAI and canopy productivity. JULES, had the smallest GPP-LAI feedback, contrasting ED2 which had greater fractional reduction in LAI than GPP (Figure 3c), despite low absolute values of LAI (Figure 2). Reductions in LAI in ED2 are strongly related to drought at all temperatures, caused by greater mortality and leaf shedding in the drought simulations (see Figure 6 in Powell et al., 2013).~~

~~We find a continuum of temperature versus drought sensitivity amongst the models. If~~

~~temperature versus drought sensitivity is expressed as the equivalent temperature increase necessary to produce the same GPP loss as in the ambient T_{air} drought simulation (50% reduction in wet season rainfall; Table 2), a low equivalent temperature would represent a greater GPP sensitivity to temperature increase and/or a lower GPP sensitivity to drought. Likewise a higher equivalent temperature represents a lower GPP sensitivity to temperature increase and/or a higher GPP sensitivity to drought. The equivalent temperature increase to reproduce the GPP loss with drought was lowest in SPA (4.92˚C), moderate in JULES and CLM3.5 (8.61˚C and 8.83˚C, respectively), and highest in SiB3 and ED2 (15.70˚C and 17.50˚C, respectively; Table 2). However across all the models a 5˚C reduction in ambient T_{air} resulted in an increase in forest productivity as GPP rose between 3.3-8.7 Mg C ha^{-1} yr^{-1} in all models (Table 2).~~

3.2 ~~Leaf scale~~Leaf-scale ~~-~~responses

~~Leaf scale A_n and g_s oppose LAI responses; the model with the smallest change in LAI (ED2) has the highest A_n and the model with the largest change in LAI (CLM3.5) has the lowest A_n (Figures 2 and 4). Similarly the models with no or limited responses of LAI to temperature change (SiB3 and ED2; Figure 2), showed the strongest responses of A_n to temperature change (Figure 4). Such trade-offs result in high model variation in the shape and magnitude of the temperature responses of A_n, g_s, transpiration (ET) and V_{cmax} (Figure 4 and 5). As T_{leaf} increases from 25˚C to 40˚C the inter-model range of A_n values increases 1.9 times from 1.65 µmol m^{-2} s^{-1} to 3.16 µmol m^{-2} s^{-1} (Figure 4a), indicating greater uncertainty of A_n at higher temperatures. The optimum A_n in SPA, SiB3, JULES, CLM3.5 and ED2 occurs at T_{leaf} values~~

~~of 25˚C, 26˚C, 27˚C, 30˚C and 30˚C respectively (Figure 4a) and significantly before the optimum point on V_{cmax} (Figure 5). In all models the A_n optimum is linked to g_s and the decline in canopy average A_n occurs at, or within, 1˚C of the T_{leaf} at which g_s starts to decline (Figure 4a-b). At T_{leaf} >25˚C the variability between the model responses of V_{cmax} increases (Figure 5). In CLM3.5, ED2, JULES, SiB3 and SPA the V_{cmax} optima was set to 35˚C, 40˚C, 32˚C, 36˚C and 30˚C respectively (10˚C of variation). Between the models there is a large variation in how quickly V_{cmax} declined following the optima; in CLM3.5 V_{cmax} declined 50% at 9˚C over the optimum, contrasting with the same decline only after 17˚C over the optimum in SPA (Figure 5).~~

~~There was high variability in the magnitude and temperature response of g_s across the models. The maximum canopy average g_s values in SiB3 (486 mmol m^{-2} s^{-1} at 25˚C) and ED2 (384 mmol m^{-2} s^{-1} at 23˚C) are substantially higher than CLM3.5 (49 mmol m^{-2} s^{-1} at 20˚C), JULES (70 mmol m^{-2} s^{-1} at 25˚C) and SPA (200 mmol m^{-2} s^{-1} at 24 ˚C; Figure 4b). Declining g_s causes the steepest decline in *ET* in CLM3.5 and SPA after 35˚C and 30˚C respectively (Figure 4c). In CLM3.5 a strong constriction in *ET* is caused by the strong influence of β on g_s (Figure 4d). β is reduced by 85±31% in CLM3.5 as T_{leaf} increase from 30-40 ˚C. The decline in β over the same T_{leaf} range was only 14±1% in ED2, 38±5% in JULES and 7.9±1% in SiB3 (Figure 4d).~~

~~For each model there are apparent, but variable, relationships between g_s and A_n (Figure 6), but no obvious relationships between A_n and V_{cmax} (Figure 7). The slope of A_n against g_s indicates intrinsic water use efficiency (IWUE); if a linear fit is forced through the g_s and A_n data for each model temperature simulation, it is apparent that all models simulate increasing~~

~~IWUE with increasing leaf temperature. The increase in IWUE from the lowest to the highest temperature simulation is higher in the drought than control simulations in all models; however there is high variability in the g_s and A_n slope when drought and control simulations of the same temperature are directly compared. Some models have lower IWUE in the drought simulations at all temperatures (CLM3.5, SPA), others have higher IWUE in the drought simulations at all temperatures (SiB3) and others (ED2 and JULES) start off with higher IWUE in the control simulations at the lower temperature simulations but switch to higher IWUE in the drought simulations at high temperature simulations (Table 3;Figure 6).~~

~~When the effect of soil water stress is removed and sunlit leaf level values are compared to the DG data for the models which could output sunlit leaf only values of g_s and A_n (SPA and CLM3.5; Figure 8), the peak A_n of sunlit leaves in SPA at 25˚C (8.72±0.24 µmol m^{-2} s^{-1}) is similar to the peak in the DG leaf scale data at 30.5˚C (8.44±0.17 µmol m^{-2} s^{-1}; Figure 8a). In CLM3.5 the peak A_n at 29˚C is considerably higher (13.48±0.20 µmol m^{-2} s^{-1}), although it occurs at a similar temperature to the observed peak, but both CLM3.5 and SPA show a decline of A_n with temperature similar to the data. Modelled g_s, however, shows a poor match to the observations (Figure 8b). Peak g_s values occur at substantially lower T_{leaf} values in CLM3.5 (27˚C) and SPA (25˚C) than observed (33.5˚C; Figure 5b). The peak sunlit g_s in SPA are also significantly higher (434±88 mmol m^{-2} s^{-1}) than the observations (123±4 mmol m^{-2} s^{-1}) and show a very sharp decline not observed in the data (Figure 8b).~~

Leaf-scale A_n and g_s oppose LAI responses; the model with the largest change in LAI in response to temperature increase (CLM3.5) has the lowest A_n values and the models with the smallest change in LAI (ED2, JULES & SiB3) have the greatest A_n values and the strongest responses of A_n to temperature change (Figure 4). Model uncertainty increases with temperature for A_n and V_{cmax} (Figure 4a & 5). For V_{cmax} this is caused by substantial variation in the optima (10˚C; Figure 5) and the rate of decline in V_{cmax} following the optima; in CLM3.5 V_{cmax} declines 50% at 9˚C over the optimum, contrasting with the same decline 17˚C over the optimum in SPA (Figure 5).

The optimum A_n in SPA, SiB3, JULES, CLM3.5 and ED2 occurs at T_{leaf} values of 25˚C, 26˚C, 27˚C, 30˚C and 30˚C respectively (Figure 4a) and significantly before the optimum point on V_{cmax} (Figure 5). In all models the A_n optimum and the initial decline in canopy average A_n is linked to declines in g_s (Figure 4a-b). Consequently for each model there are apparent, but variable, relationships between g_s and A_n (Figure 6), but no obvious relationships between A_n and V_{cmax} (Figure 7).

There was high variability in the magnitude and temperature response of g_s across the models. The maximum canopy average g_s values in SiB3 (486 mmol m^{-2} s^{-1} at 25˚C) and ED2 (384 mmol m^{-2} s^{-1} at 23˚C) are substantially higher than CLM3.5 (49 mmol m^{-2} s^{-1} at 20˚C), JULES (70 mmol m^{-2} s^{-1} at 25˚C) and SPA (200 mmol m^{-2} s^{-1} at 24˚C; Figure 4b). In CLM3.5 a strong constriction in *ET* is caused by the strong influence of β on g_s (Figure 4c-d). β is reduced by 85±31% in CLM3.5 as T_{leaf} increase from 30-40 ˚C. The decline in β over the same T_{leaf} range was only 14±1% in ED2, 38±5% in JULES and 7.9±1% in SiB3 (Figure 4d).

The slope of A_n against g_s indicates intrinsic water use efficiency (IWUE): the rate of increase of assimilation per unit increase in g_s. If A_n is plotted against g_s separately for each model temperature simulations (-5˚C, 0˚C, +2˚C, +4˚C, +6˚C) and a linear fit is forced through the g_s and A_n data, it is apparent that all models simulate increasing IWUE (an increase in slope) from the -5˚C up to the +6˚C simulations (Figure 6 & Table 3). The increase in slope of A_n and g_s from the -5˚C to +6˚C temperature simulation is greater in the drought than control simulations in all models (Figure 6 & Table 3), suggesting that both increasing temperature and reduced water availability increase IWUE.

When the effect of soil water stress is removed and sunlit leaf level values are compared to the DG data for the models which could output separate sunlit leaf values of g_s and A_n (only SPA and CLM3.5; Figure 8), the peak A_n of sunlit leaves in SPA at 25˚C (8.72±0.24 µmol m^{-2} s^{-1}) is similar to the peak in the DG leaf-scale data at 30.5˚C (8.44±0.17 µmol m^{-2} s^{-1}; Figure 8a). In CLM3.5 the peak A_n at 29˚C is considerably higher (13.48±0.20 µmol m^{-2} s^{-1}), although it occurs at a similar temperature to the observed peak. Both CLM3.5 and SPA show a decline of A_n with temperature similar to the data. Modelled g_s, however, shows a poor match to the observations (Figure 8b). Peak g_s values occur at substantially lower T_{leaf} values in CLM3.5 (27˚C) and SPA (25˚C) than observed (33.5˚C; Figure 5b). The peak sunlit g_s in SPA are also significantly higher (434±88 mmol m^{-2} s^{-1}) than the observations (123±4 mmol m^{-2} s^{-1}) and show a very sharp decline not observed in the data (Figure 8b).

4 Discussion

4.1 Canopy- and leaf-scale feedbacks

The response of NEE and GPP to short-term changes in temperature ~~was~~ demonstrated substantially greater consistency across models than ~~that of~~for LAI (Figure 2). ~~Within~~ Amongst the models which had dynamic LAI, the change in LAI from the original value ranged from 4.5 m^2 m^{-2} in SPA to 1.0 m^2 m^{-2} in ED2. Interestingly, the change of LAI with T_{air} in ED2~~,~~ and JULES was so low that it ~~and~~ was more comparable to ~~SiB3~~ SiB3, a model with fixed LAI. This contrasts CLMA3.5 and SPA, within which LAI declined substantially as T_{air} rose above a threshold (Figure 2d). ~~all showed very little change in absolute LAI values with changes in temperature, despite the fact that ED2 and JULES are dynamic vegetation models and SiB3 does not have dynamic LAI. This is contrasted with a sharp decrease in LAI in response to changes in temperature in CLM3.5 and SPA (Figure 2d).~~ The inter-model~~inter-~~ range in LAI ~~values across the 5 models~~ (maximum range 7.5 m^2 m^{-2}) was ~~however~~ greater than ~~any~~ the decline in LAI with T_{air} in any model. If leaf~~-~~-scale fluxes are scaled using an inaccurate LAI, the simulation of both accurate leaf- and canopy~~-~~-scale fluxes is not possible (Bonan et al., 2012; Lloyd et al., 2010; Mercado et al., 2006; Mercado et al., 2009). Given the large variability in LAI responses across the models, it would be expected that there should be a greater variability in GPP and NEE than was observed. ~~Models~~ Therefore the models ~~have to~~must compensate for variability in canopy structural parameters, such as LAI, through adjustment in other ~~leaf scale~~leaf-scale parameters if the observed consistency in ecosystem-scale responses is to be maintained (Bonan *et al.,* 2012). ~~We therefore suggest that the variability in LAI responses is compensated for by variations in parameterisation at the leaf scale, which in turn drive similarly high variation in the leaf scale fluxes.~~

We found substantial variation in the magnitude and temperature responses of leaf~~-~~-scale parameters: peak V_{cmax} had a 10°C T_{leaf} range across the models (Figure 5), g_{s} values varied by over an order of magnitude (Figure 4b), the inter-model range of β and ET ~~values showing increasingly large disparities with increasing~~increased with T_{leaf} (Figure 4c-d), and there was a two-fold increase in the inter-~~modal~~ model ~~A_n~~–range of A_n ~~had a two fold increase between~~as T_{leaf} ~~values of~~rose from 25-40°C (Figure 4a). Such variability across the models suggests that any ~~similarities~~ similarity in the response~~s~~ of NEE to T_{air} ~~temperature between~~ among models ~~are~~ is caused by different processes ~~having differing~~and feedbacks at the leaf-scale. Had the models been run to their equilibrium states, it is likely that there would have been greater divergence of model responses at ~~the~~ both canopy- and leaf--scales. Prolonged higher temperatures reduce long-term moisture availability and cause more severe changes in β; in dynamic PFT-models this can result in a substantial shift of PFT away from tropical forest. Without more data to evaluate which models ~~are producingprodcued~~produced ~~both~~ the correct ~~V_{cmax} and g_s,~~ responses to temperature, it is hard to have confidence in predictions of climate change impacts in Amazonian ~~simulated by either one or multiple.~~ ~~models.~~

Variability in the control of g_s and leaf biochemistry on A_n and changes in IWUE efficiency with increasing temperature or drought will have significant consequences on the demand of water from a forest (Harper et al., 2014). In this study we find g_s had a greater control on the change in A_n with increasing temperature because: A_n started to decline at T_{leaf} values which were lower than those at which peak V_{cmax} occurred (Figure 4b and Figure 5) and A_n maintained a positive relationship with g_s across all models (Table 3; Figure 6), but no clear relationship with V_{cmax} (Figure 7). All the models in this study also predicted an increases in IWUE from the lowest (ambient T_{air} -5°C) to the highest (ambient T_{air} +6°C) temperature simulation; this increase in IWUE was also always greater in the drought temperature simulations relative to the control temperature simulations (Table 3; Figure 6). Increases in IWUE with increasing temperature suggests that as the ecosystem warms A_n will become more sensitive to reductions in g_s and g_s will maintain a greater control on A_n than biochemical controls, even at very extreme increases in temperature (ambient T_{air} +6˚C).

These results are consistent with the hypothesis that temperature increases will mainly be manifest~~ed~~ through the effect of increased VPD on stomatal conductance (Lloyd and Farquhar 2008). They are also consistent ~~and~~ with leaf warming data from the Tapajos forest which show that reductions in A_{n} start to occur at 4-5°C before the optimum point for V_{cmax} and J_{max} in sunlit leaves (Tribuzy, 2005). However the responses from longer~~–~~-term leaf warming experiments at the same site showed that changes in leaf biochemistry with increasing leaf temperatures was an important control on A_{n} (Doughty 2011), suggesting more data ~~is~~ are required to ~~effectively~~ test effectively both the short and long term responses of A_{n} to changes in temperature in models.

Comparing the short term direct effect of temperature on the A_{n}-g_{s} relationships is complicated because of the differences in the calculation and implementation of the effect of water stress amongst models (Powell et al., 2013; Zhou et al., 2013). β is altered by changes in SWC, which can be caused by changes in temperature (via increased VPD altering SWC), as well as changes in precipitation; in turn β alters both g_{s} (Figure S1) and A_{n}. The decrease in β with temperature increase was highly variable ~~between~~among models (Figure 4d). Consequently, the direct influence of soil water stress on g_{s}, A_{n} and *ET*, versus the indirect effect of VPD, was inconsistent between models. Resolving these inconsistencies is important, as water stress functions impact the ratio of modelled latent to sensible heat fluxes and so when coupled to global climate models they alter climate and vegetation feedbacks (Harper et al., 2014). Improving how water stress is simulated in models is therefore essential to improving temperature and drought responses in tropical forests.

~~The models did agree that reductions in g_s with increasing temperature were the main cause of reductions in forest productivity (Lloyd and Farquhar, 2008). A_n decline was related to g_s decline (Table 3; Figure 6), but not V_{cmax} decline (Figure 7) and the decline in A_n with increasing T_{leaf} occurred prior to the T_{leaf} peak in V_{cmax} (Figure 4b and Figure 5). The slope of A_n-g_s reflects IWUE and our study demonstrates that all the models predict an increase in IWUE with rising leaf temperatures and an accentuation of this change under drought conditions (Table 3; Figure 6). Very steep A_n-g_s slopes at higher leaf temperatures suggests that as the ecosystem warms A_n becomes more sensitive to reductions in g_s, and therefore that stomatal controls are likely to have greater influence at higher temperatures; this suggests that even at high temperatures (up to 6˚C above ambient) reductions in A_n are caused mainly by stomatal, rather than a biochemical responses. These results reflect patterns found in leaf warming data from the Tapajos forest which show that reductions in A_n start to occur at 4-5°C before the optimum point for V_{cmax} and J_{max} in sunlit leaves (Tribuzy, 2005), but not the responses of other longer term leaf warming experiments at the same site which experienced changes in leaf biochemistry with increasing leaf temperatures (Doughty 2011). Substantially more data is therefore required to effectively test such results.~~

~~IWUE was highly variable across the models, particularly with the introduction of precipitation change (Table 3; Figure 6). Variability in the A_n-g_s relationships are related to differences in how β is calculated by models (Powell et al., 2013; Zhou et al., 2013), as β alters g_s (Figure S1) and A_n. β is altered by changes in SWC which can be caused by changes in temperature (via increased VPD altering SWC), as well as changes in precipitation. The decrease in β with temperature increase was highly variable between models (Figure 4d).~~

~~Consequently, the direct influence of soil water stress on g_s, A_n and ET, versus the indirect effect of VPD, as temperature and precipitation changed was inconsistent between models. Resolving these inconsistencies is important, as water stress functions impact the ratio of modelled latent to sensible heat fluxes and so when coupled to global climate models they alter climate and vegetation feedbacks (Harper et al., 2014). Improving how water stress is simulated in models is therefore essential to improving temperature and drought responses in tropical forests.~~

~~When considering SPA, a model that uses a more mechanistic water stress response~~When ~~(and~~ focusing only on periods of high soil water content ~~to~~ and ~~remove~~ therefore removing the effects of water stress~~,~~ ~~response of~~ A_n~~)~~ and~~,~~ g_s values from fully sunlit leaves still varied substantially from the response and magnitude of the DG data (Figure 8). Given the DG data ~~was~~ were averaged from only three top-~~-~~canopy species,~~compared to deriving from all sunlit leaves in CLM3.5 and SPA,~~ some degree of variation~~s~~ between the model and the data is expected. ~~However, t~~The variability between the peak data and peak model g_s ~~is~~ was however > 4 times (Figure 8b) and the modelled temperature optima for g_s (25-27˚C) was substantial lower than observed by DG (33.5˚C).~~Had the modelled temperature optima for g_s been closer to the observed temperature optima (33.5˚C), V_{cmax}, may have had a greater limitation on A_n, as at the observed g_s temperature optima (33.5˚C) some models are past the V_{cmax} temperature optimum (Figure 5). Consequently in this study the dominance of the effect of g_s on photosynthesis may be derived from low g_s optima in the models.~~

Given that CLM3.5 and SPA are in the lower range of the total model variability for the g_s and A_n of an average canopy leaf (aggregated sunlit and shaded leaf; Figure 4a-b), the variation from the data is likely to be substantially larger if sunlit leaf data could be extracted from all models. Considering the importance of g_s in controlling leaf productivity, the suitability of the empirical models of g_s used in these models requires further testing (Bonan *et al.*, 2014). The use of optimised rather than empirical models may provide an opportunity to improve the capability to simulate g_s responses to temperature and water stress in greater detail (Heroult et al., 2013; Medlyn et al., 2013; Medlyn et al., 2011; Zhou et al., 2013).

4.2 Combined drought and temperature sensitivities

Previous modelling studies have shown that there is high variability in how sensitive models are to temperature and drought (Friedlingstein et al., 2006; Galbraith et al., 2010; Luo et al., 2008; Sitch et al., 2008), but that vegetation models have embedded in them greater sensitivity to rises in temperature than drought (Galbraith et al., 2010) despite the evidence for strong drought sensitivity in natural rainforests (Gatti et al. 2014~~; Meir et al. 2015~~). The responses of modelled forest production in this study to combined changes in precipitation and temperature ~~was~~ were however highly variable. ~~Rising T_{air} in~~ CLM3.5 and SPA had~~caused~~ very strong compound effects of temperature on drought-~~-~~induced reductions in GPP, R_{eco} and LAI (Figure 3) relative to JULES and SiB3. ~~. In~~ In ED2, the drought effect on GPP ~~was~~ was always stronger than the ~~other models~~temperature effect (Figure 3) ~~because of~~because it has a ~~a~~ strong drought-mortality effect at this site (Powell et al., 2013)~~; da Costa et al. 2010)~~. ~~Considerable model disparity in the response of A_n and LAI to drought and temperature (Figures 2, 4 and 6) resulted in substantial variation in relative sensitivity of models to temperature and drought.~~ ~~Previous modelling studies have shown that there is high~~

~~variability in how sensitive models are to temperature and drought (Friedlingstein et al., 2006; Galbraith et al., 2010; Luo et al., 2008; Sitch et al., 2008), but that vegetation models have greater sensitivity to rises in temperature than drought (Galbraith et al., 2010).~~ This study demonstrates that there is ~~actually~~ a continuum in model responses from models that require a low increase in ambient T_{air} to cause the same GPP loss as a 50% reduction in wet season rainfall (SPA, 4.9 ˚C), to models that have a very strong drought response and therefore require a substantial increase in ambient T_{air} to replicate the same GPP loss as a 50% reduction in wet season rainfall (ED2, 17.5 ˚C; Table 2). As a 6˚C rise in temperature and a 50 % reduction in rainfall are changes which may occur in Amazonia during the 21st century (Christensen et al, 2007; Collins et al., 2013), we suggest that there is currently no consensus ~~between~~ among vegetation models as to whether there will be a stronger drought or temperature response to future climate change within tropical forests.

Across all the models~~, the dominance of stomatal control on productivity resulted in~~ GPP ~~increasing~~ increased when ambient T_{air} was reduced by 5˚C; this ~~was~~ occurred because the ~~and the~~ambient air temperature -5˚C ~~temperature was~~was closer to the modelled g_s ~~optimum~~optima. This result suggests models are currently predicting that Amazonian forests are operating beyond a temperature and VPD optimum. Given that the models underestimate the point at which NEE declines with T_{air} by 3-6˚C and the point at which g_s declines with T_{leaf} by 7.5-9.5˚C (Figure 2 and 4), it ~~is~~ seems likely that the models in this study may be biased towards temperature calibrations for temperate ecosystems. Consequently, as well as moving towards implementing more mechanistic responses to improve models, more research to test and adjust their temperature responses in tropical ecosystem is necessary. The range of model responses in this study is likely to stem from real uncertainty in our understanding of the responses by tropical rain forest ecosystems to changes in precipitation and temperature. Further analysis of the same questions using models that vary in complexity (eg, statistical or optimised models, as well as purely mechanistic) might provide additional insight into mechanistic and simulation bias (systematic or random), as well advancing understanding about climate risk that we derive from them (Meir, Mencuccini and Dewar, 2015)

5 Conclusion

This is the first study in which canopy and leaf temperature responses from multiple vegetation models are analysed and compared to existing data on leaf and canopy temperature responses from a tropical forest site. This study finds models lie along a continuum of those which have a greater sensitivity of GPP to changes in temperature relative to drought and those which have a greater sensitivity to drought relative to a change in temperature. Any consistency in model responses to temperature and drought were however, the result of inconsistent leaf-scale responses, which were found to compensate~~ing~~ for substantial inter-model variation in the magnitude and response of LAI to drought and temperature.

All the models in this study predict that reductions in A_n are dominated by stomatal rather than biochemical responses and that ~~tropical forest productivity will become more sensitive to reductions in g_s as temperatures rise~~IWUE increased with rising temperatures. The dominance of the effect of g_s rather than V_{cmax} on A_n results in all the models predicting greater forest productivity when temperatures are 5°C below ambient and closer the temperature of the g_s optimum. ~~Despite consistent prediction of increasing IWUE with temperature rise, there was however no consistency between models in how IWUE will respond to combined changes in temperature and drought. It seems therefore that the consistency of model responses is reduced as changes in multiple climate variables are introduced simultaneously.~~This suggests that currently models predict that tropical forests are operating beyond a temperature and VPD optimum, but we note that these predictions may be influenced by parameterisations derived originally from temperate zone forests.

~~To~~This study concludes that to ~~effectively~~ simulate effectively the response of the Amazon forest to changes in multiple climatic factors substantial improvements are needed in how leaf-~~–~~scale processes and leaf-~~–~~to-~~–~~canopy scaling are simulated. Further ~~measurement campaigns~~ observational data are also required to generate consistent leaf- and canopy-~~–~~scale data for independent model evaluation.

Author Contributions

L. R. and M. W. designed the experiment, performed simulations, analysed data and prepared the manuscript. A. H., B. O. C., D. R. G., H. M. A. I., T. L. P., S. S, P. M. performed simulation, contributed to study design and prepared manuscript. D. D. contributed to the data analysis. N. L. and Y. M. contributed to the study design. P. M.~~ designed the experiment,~~ contributed to data analysis and prepared the manuscript.

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Table 1: Summary of the characteristics of each of the ~~four~~ five vegetation models (CLM3.5, ED2, JULES, SiB3, & SPA).

	CLM3.5	**ED2**	**JULES**	**SiB3**	**SPA**
No° of plant function types	5	4	10	1	1
Canopy structure	Big-leaf	Gap model	Layered Canopy	Big-leaf	Layered canopy
Leaf Area index	Dynamic	Dynamic	Dynamic	Fixed	Dynamic
Division of sunlit and shaded leaf	Y (discrete division)	N	N	N	Y (discrete division)
Simulation of water stress on A_n and g_s.	Water stress factor	Water stress factor	Water stress factor	Water stress factor	Linked soil-leaf water potential/resistance model to g_s model.
Origin of photosynthesis model	Farquhar et al., (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al., (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al., (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al., 1(980); Farquhar and Sharkey (1982) Collatz et al. (1991)	Farquhar et al., (1980); Kirschbaum and Farquhar (1984); McMurtrie et al. (1992)
Key model references	Bonan et al., (2003); Levis et al., (2004); Oleson et al. (2008).	Medvigy et al., (2009); Kim et al 2012.	Best et al., (2011); Clark et al., (2011)	Sellers et al., (1992); Sellers et al., (1996); Baker et al (2008).	Williams, (1996); Williams et al., (2005); Fisher et al., (2006)

Table 2: Model values for GPP (Mg C ha^{-1} yr^{-1}) for the last year (2006) of the ambient air temperature control plot simulation (T_{air} +0°C), the control plot simulation -5°C (T_{air} -5°C), the control plot simulation +6°C (T_{air} +6°C) and the ambient air temperature drought plot simulation (T_{air} +0°C). The equivalent temperature is the elevation in the control plot simulation temperature needed to replicate the same magnitude reduction in GPP as the drought simulation, for the year 2006 and at ambient temperatures. The equivalent temperature is derived from a linear relationship between GPP values in 2006 and the air temperatures in the 5 temperature simulations per model.

	CLM3.5	ED2	JULES	SiB3	SPA
Control GPP T_{air} -5°C	40.74	31.74	36.73	35.27	38.23
Control GPP T_{air} +0°C	36.68	28.31	31.16	31.95	29.55
Control GPP T_{air} +6°C	28.03	20.70	20.08	27.50	15.89
Drought GPP T_{air} +0°C	26.47	10.79	18.13	20.86	19.55
Equivalent T_{air}	8.83	17.50	8.61	15.70	4.92

Table 3: Values show the normalised intrinsic water use efficiency (IWUE) calculated from the linear slope of normalised A_n plotted against normalised g_s (Figure 6). The normalised IWUE is calculated separately for each models' control and drought temperature simulations (ambient air temperature (T_{air}) -5˚C, +0 ˚C, +2 ˚C,+4 ˚C, and +6 ˚C). [Note NA in CLM3.5 drought simulations indicates the model changed from a forest to a grassland]

~~The slope of the relationships of A_n with g_s (intrinsic water use efficiency; IWUE), shown in Figure 6 for each temperature run (ambient air temperature (T_{air} -5˚C, +0 ˚C,+2 ˚C,+4 ˚C, and +6 ˚C) in the control and drought simulations (panels f-j), for each model. [Note NA in CLM3.5 drought simulations indicates the model changes to a grassland].~~

	Control Simulations					Drought Simulations				
	CLM3.5	ED2	JULES	SiB3	SPA	CLM3.5	ED2	JULES	SiB3	SPA
T_{air} -5˚C	0.84	0.42	0.50	0.09	0.49	0.73	0.29	0.50	0.10	0.27
T_{air} +0˚C	0.93	0.56	0.83	0.49	0.68	0.93	0.40	0.60	0.93	0.24
T_{air} +2˚C	1.01	0.67	1.01	0.58	0.73	1.08	0.53	0.97	1.11	0.41
T_{air} +4˚C	1.05	0.79	1.18	0.65	1.00	NA	0.78	1.37	1.20	0.74
T_{air} +6˚C	1.11	0.95	1.32	0.69	1.50	NA	1.10	1.73	1.22	1.15

Figure captions:

Figure 1: Schematic diagram showing how droughts, via the combined effects of increased air temperature (T) and ~~reductions in~~reduced precipitation (PPT), affect the carbon cycle of a tropical forest, including the effects on: vapour pressure deficit (VPD), evapo-transpiration (E_t), stomatal conductance (g_s), soil water content (SWC), net photosynthesis (A_n), leaf area index (LAI), the maximum rates of RuBP carboxylation and electron transport (V_{cmax} and J_{max} respectively), autotrophic respiration (R_a) heterotrophic respiration (R_h), gross primary productivity (GPP), and net ecosystem exchange (NEE). + signs indicates a positive feedback effect between variables (i.e. an increase in one variable can only cause an increase in another if all else is equal), - signs indicate a negative feedback effect, and +/- indicate the possibility of both a positive and negative effect. Solid arrows represent responses which occur over short timescales of minutes to hours, whereas dashes arrows represent responses which can occur over longer timescales from days to months.

Figure 2: Comparison of the air temperature (T_{air} °C) response of a) daytime net ecosystem exchange (NEE, µmol m^{-2} s^{-1} ; note that negative values of NEE indicate carbon sequestration), b) gross primary productivity (GPP, µmol m^{-2} s^{-1}), c) ecosystem respiration (R_{eco} (µmol m^{-2} s^{-1}), d) leaf area index (LAI, m^2 m^{-2}). The lines show the median model responses from the five control temperature runs per model pooled and divided into 1-°C temperature bins. The grey shaded area shows the combined 15.9th and 84.1th quantiles for all models. The black points and error bars in panel a) show the daytime eddy-flux inferred NEE (cf. Figure 4 in Doughty and Goulden 2008).

Figure 3: Modelled effect of short-term changes in temperature and drought. ~~Fractional~~

~~change in~~Changes in: a) gross primary productivity (GPP) b) ecosystem respiration (R_{eco}) and c) leaf area index (LAI) i~~o~~n the final year (2006) in the drought run ~~relative to the~~expressed as a fraction of the value in the final year (2006) of the control run, ~~are shown~~ for the T_{air} -5˚C (grey bars) and T_{air} +6˚C (w~~W~~hite bars) simulations.

Figure 4: Comparison of the dry season mean (sunlit + shaded leaves, weighted by their respective LAIs) leaf-level response to temperature ($T_{leaf;}$ °C) of a) net photosynthesis (A_n, µmol m^{-2} s^{-1}), b) stomatal conductance (g_s, mmol m^{-2} s^{-1}), c) leaf transpiration (E_t, mm m^{-2} s^{-1}), and d) the soil water stress factor (β) for average canopy leaves [Note SPA does not simulate β] . The lines show the median model responses from the control plot for the five temperature simulations pooled and divided into 1 °C temperature bins for each model. The grey shaded area shows the combined 15.9th and 84.1th quantiles for all models. [Note JULES Et data is missing from these ~~runs~~simulations]

Figure 5: The temperature response of V_{cmax} for each model shown relative to the V_{cmax} at 25 °C per model.

Figure 6: The relationship between 30 minute values of modelled ~~dry season~~ stomatal conductance (g_s) and photosynthesis (A_n) normalised by their respective maximum values; -A_n and g_s values are taken only from the dry season when PPFD > 1000 µmol m^{-2} s^{-1} ~~when PPFD > 1000 µmol m^{-2} s^{-1}~~. Values are ~~shown for each~~coloured separately from deep blue to red (see legend) for each temperature ~~run~~ simulations (ambient air temperature -5˚C, +0 ˚C,+2 ˚C,+4 ˚C, and +6 ˚C) and panels ~~in~~separate the control (panels a-e) and drought simulations (panels f-j), for each model. Values are from sunlit and shaded leaves, weighted by their respective LAIs. A separate linear line is ~~forced~~ plotted through the normalised A_n~~-~~,

g_s -data for each temperature ~~run~~ simulations, the slope of which represents the normalised intrinsic water use efficiency: the normalised increase in A_n per unit increase in normalised g_s. ~~to indicate the steepness of the slope, which represents intrinsic water use efficiency.~~ L~~Data and l~~inear lines are also coloured from deep blue to deep red to differentiate the additions to ambient air temperature (see legend).

Figure 7: The relationship between V_{cmax} (μmol m^{-2} s^{-1}) and photosynthesis (A_n mmol m^{-2} s^{-1}) for the half hourly output from each model in the dry season of the control runs, with PPFD > 1000 μmol m^{-2} s^{-1}. Values are from sunlit and shaded leaves, weighted by their respective LAIs. Results are shown across all leaf temperatures explored in this study (colour change from blue to red ~~indicated~~ indicates increasing leaf temperature (see legend)).

Figure 8: The sunlit leaf-level response of dry season a) net photosynthesis (A_n, μmol m^{-2} s^{-1}) and b) stomatal conductance (g_s, μmol m^{-2} s^{-1}) to leaf temperature ($T_{leaf;}$ °C) for CLM3.5 (orange) and SPA (red). The lines show the median model responses from the control plot for the five temperature simulations pooled and divided into 1 °C temperature bins for each model. The shaded areas around each line show the 15.9th and 84.1th quantiles for each model. Data from Doughty and Goulden is shown as black points; error bars show the standard error. [Note only SPA and CLM3.5 output data on sunlit leaf values of A_n and g_s.]

Figure S1: The relationship between β and stomatal conductance (g_s mmol m^{-2} s^{-1}) for each model in the dry season, with PPFD > 1000 μmol m^{-2} s^{-1}. Values are from sunlit and shaded leaves, weighted by their respective LAIs. Results are shown across all leaf temperatures explored in this study (colour change from blue to red indicated increasing leaf temperature) and separately for the drought and control simulation.