**We appreciate and are thankful for the reviewers’ thoughtful comments and believe the manuscript is much improved as a result of addressing their comments. We did not incorporate Reviewer 2’s first comment on comparing enzyme data to leaf-level data as we feel that no leaf-level data collected to date are appropriate for comparison to enzyme-level data. This is due to issues in the estimation of mesophyll conductance, cuticle conductance, boundary layer conductance (all of which affect the estimate of chloroplastic CO2), the photorespiratory CO2 compensation point (Γ\*, which requires the previous three parameters to properly estimate – while Sc/o could be used, this value should be measured independently at the leaf level as the differences between in vitro and in vivo environments could cause differences in measured values at each scale), and light respiration (which, as the Editor is aware, is still poorly understood relative to dark respiration). In our correspondence on this point with Dr. Robert Sharwood, we concluded that there are no satisfactory comparisons available in the literature. As well, we feel that including such a comparison would detract from the focus of the manuscript – i.e. the derivation error. We do note however, that data on the kcat of rubisco from Sharwood et al. (2016) show activation energies that fall within the range of Vcmax activation energies estimated at the leaf level.**

**Our responses are below in bold. Line numbers refer to the manuscript version with all changes accepted.**

Editor’s Comments

Each reviewer has provided detailed, thoughtful comments, which when addressed, should result in substantial improvement of the manuscript.  Reviewer 1 askes that you help readers follow the Johnson and Medlyn formulations via use of abbreviated terms.  I agree with Reviewer 1 that an earlier harmonization of Eqn 10 with earlier equations would help, and that it would worth considering adding a two panel figure of Vcmax.25 and Jmax.25 scaled over a wide range of temperatures.  Please also consider revising the final paragraph.

**We have switched to using M2002 and J1942 as suggested by Reviewer 1. Regarding the two-panel figure, we think that this would simply be a repeat of panels c-f in Figure 1 (formerly Figure 2) where we show the fitted equation and data across a broad range of temperatures (10 – 50 Celsius in one case). We have also revised the final paragraph – see reviewer responses below and lines 305-323.**  
  
Reviewer 2 makes a nice suggestion – that being to look at studies that apply the T response functions to enzymatic reaction data.  Like Reviewer 1, this reviewer also felt that some change was needed at the end of the manuscript, with Reviewer 2 on what future needs to be done.

**We did not incorporate Reviewer 2’s first comment on comparing enzyme data to leaf-level data as we feel that no leaf-level data collected to date are appropriate for comparison to enzyme-level data due to issues in the estimation of mesophyll conductance, cuticle conductance, boundary layer conductance (all 3 of which affect the estimate of chloroplastic CO2), the photorespiratory CO2 compensation point (Γ\*, which requires the previous three parameters to properly estimate – while Sc/o could be used, this value should be measured independently at the leaf level), and light respiration (which, as the Editor is aware, is still poorly understood relative to dark respiration). As well, we feel that including such a comparison would detract from the focus of the manuscript – i.e. the derivation error. As stated, we have modified the final paragraph (lines 305-323).**  
  
Reviewer 3 makes a great suggestion regarding the need to document how Eqn 3 was used post 1942 in order to identify when the temperature term was dropped. Given the importance of the equations for future modelling, please also do a final check of the algebra (noting that Reviewer 3 is a mathematician).

**We have followed Reviewer 3’s suggestion and traced the omission (see our response below). We have also rechecked our algebra to ensure that the derivation is correct.**

Reviewer 1’s Comments

Murphy & Stinziano have uncovered a derivation error in a widely used Arrhenius function that resulted in a dropped term.  They examined the impact of this error by comparing the original (1942) formulation with a modern formulation using a publicly available database of A-Ci curves to evaluate the effect on fitted parameters. Their key finding was that the fitted activation energy (Ea) differed between the original and modern formulations and could result in a marked deviation in modeled daily CO2 assimilation. This is a really nice piece of detective work, the authors make a clear case that the impact of this error has a far reaching effect on many process based models. The work will be broadly important to New Phytologist readers and the ripples of this paper will travel far, particularly into the terrestrial biosphere modeling community. Finding and fixing errors like this is an important contribution that domain experts can make to the modeling community and this work is a great example of just that.

**Thank you for the positive feedback!**  
  
General comments  
  
I found it unnecessarily cumbersome to keep track of which formulation was the Johnson one and which one was the Medlyn one. Perhaps the authors could consider referring to them as J1942 and M2002 or original and modern – anything to help the reader keep them straight. The explicit reference to the equations is important so retaining that on first definition of the shorthand for the two formulations would be beneficial. This particularly relevant for the figure axis labels.

**We agree with the reviewer and have since changed our notation to J1942 and M2002 so that the manuscript is easier to follow.**  
  
I think the paper would benefit from early harmonization of the terms in the equations. The authors recognize the value of this (Eqn 10) but the reader has to struggle with this until the last equation. I think clarity could be improved by harmonizing immediately and alerting the reader to the harmonization on first presentation of the original and modern equations.

**We agree and have done this – we now start the derivation with harmonized terms in Equation 5.**  
  
I think an additional figure would help broaden the appreciation of the work. It would be nice to see a two panel figure of a Vcmax.25 and Jmax.25 scaled between 5 and 45oC using the Ea from the original and modern Arrhenius functions.

**We used over 400 values of Ea, ΔS, and Hd in our modeling, making this impractical to do. However, we do have Vcmax and Jmax scaled to temperature in panels c-f of Figure 1 (formerly Figure 2), which illustrate cases where the temperature responses for M2002 and J1942 are nearly identical (e.g. Fig. 1c) and cases where they vary more (e.g. Fig. 1d).**  
  
The closing paragraph could be improved. I suggest deleting the sentence starting “Despite…” (285-287) and focusing the final paragraph on the key finding – the detection of the error, that needs to be fixed in many models and the impact of the error of model output. If the authors want to retain the brief reference to model tuning (I think) in the last phrase of the paper (289) the thought should be expanded.

**We have removed the sentence starting with “Despite…” and have expanded the discussion to include which Earth systems models are most greatly affected by the incorrect use of the M2002 equation. Lines 316-318. Note that 17 of 40 earth system models are affected in some way by this error!**  
  
The authors should reread their figures and ensure that they are describing all the graphical elements of the figures in the legends I found the legends to be incomplete.

**As far as we can tell, this comment mostly relates to Figure 1 (formerly Figure 2), to which we have added a substantial amount of description to the figure caption.**  
  
Minor comments  
  
Title   Including the citation in the title is not ideal

**We have since amended the title to exclude the citation.**  
  
26      How can a term be half dropped its either in or out, clarify the point or amend the bullet

**We agree, and have removed the word “completely”. Line 26**  
  
49      A is not a good choice for a symbol given the topic and the later use of A for photosynthesis

**We agree, and have changed “A” to a “k” to keep in with the later notation (i.e. k25). Line 50**

55-60   The order of the symbol descriptions does not align with the presentation of the equations and makes it hard for the reader

**We have changed the order of the definitions to match with the presentation of equations. Line 56 - 61**  
  
57      It would help the clarity to state degrees Kelvin (K) or similar

**Done. Line 58**  
  
68      Rogers et al (2017) considered a limited number of models. I think the impact of the paper could be improved with a table highlighting which major Earth system models (take the CMIP suite for example) have this error, or if it’s all of them then state that. I think understanding how widespread this error is in major Earth system models would increase the impact of the paper.

**We thank the reviewer for this comment and pursued this point enthusiastically – only to find out that this is not as simple a task as it appears at first glance (documentation for some of the CMIP6 models is rather terrible). We were able to sort through each of the 40 models (from, as it turns out, a total of 12 model families) to find out how photosynthesis was represented in the land surface submodels. We found that 4 land surface model families were affected, which means that 17 of the 40 CMIP6 models are currently affected by the derivation error. We include this information in a new Table 1, and discuss this on lines 316-318.**

**As a side note of potential interest to the reviewers and editor – we found 3 models using the Simple Biosphere Model that do not even consider photosynthesis!**

213-214 As a reader I struggled with this sentence and with interpreting Fig 2. I think some additional text is needed to help the reader understand the key point. Where on the figures should we be looking? Why pick these examples?

**We have modified this sentence to read “However, while some fitted temperature responses based on BIC appeared identical, there were some cases where the fitted shape differed the largest discrepancy between fitted responses was observed when comparing Jmax,25 of both plant species scaled across 10 ˚C and 50 ˚C (Figs. 2c-f; note the differences between the blue and red hatched lines)”. Line 237-238.**

**We believe our changed make our point clearer – there are cases where the temperature responses differ substantially between the two equations. The examples we show were chosen to represent both near identical fits and fits that deviated a lot between M2002 and J1942.**

Reviewer 2’s Comments

Comments to the Author  
This paper revisits the original derivation of photosynthetic temperature response from Johnson et al. (1942), and finds that current forms of the model have omitted a term (T/290.15) that they show has an impact on the value of the Ea term and up to 18% positive bias on daily carbon gain, depending on the circumstances.  
  
After reading the original reviews for a submission to a different journal and the authors' responses, I am convinced that the paper makes a strong case for revising current models of photosynthetic temperature response back to the original Johnson et al. (1942) one.  Many thanks to the authors for including these!  
  
I have only two small suggestions that might help set the results into a broader context.  
  
1. The activation energy concept was originally derived for a single chemical.  In plant science, it has always been used in the context of a process with many interacting chemicals (enzymes).  Beyond getting the photosynthetic temperature response and daily photosynthetic total correct, what does activation energy mean for a process with many interacting enzymes?  Have there been any studies of the temperature response of the pure enzyme, and, if so, how did its Ea and temperature response compare to that of the leaf or chloroplast response?

**This is an epistemological issue we have struggled with in the past. When considering Vcmax for example, CO2 concentration, rubisco concentration, rubisco activation state and rubisco activase activity could all be limiting factors, such that activation energy of Vcmax is then describing the temperature response of the rate-limiting factors for Vcmax.**

**There have been studies on single-enzyme temperature responses (mostly rubisco however – for photosynthetic electron transport, we would need temperature responses of Cyt b6/f most likely, or NADP oxidoreductase). Sharwood et al. 2016 (Figure 3 in paper, panels a, b) found activation energies of rubisco kcatc (the CO2 fixation rate, approximately equivalent to the meaning of Vcmax) of 26.4 to 69.8 kJ mol-1 across C3, C2, and C4 species (12 total species) depending on the temperature range (with a breakpoint in responses at 25 Celsius). This falls within the range of fitted Ea values for Vcmax (Figure 2a). We do not know of any papers where a temperature response of both kcatc and Vcmax were compared. Based on correspondence with rubiscologist Dr. Robert Sharwood, such a comparison doesn’t exist, likely due to the difficulty of getting a true estimate of Vcmax in vivo. This direct comparison is difficult for a few reasons: first, CO2 responses on a chloroplastic basis (A-Cc curves) are needed, along with leaf-level characterization of the photorespiratory CO2 compensation point and light respiration. Given the current methodological and philosophical difficulties in assessing a) mesophyll conductance in a 1-dimensional manner to obtain Cc estimates (not to mention the myriad assumptions required with online stable isotope analysis or the unreliability of the variable J/constant J fluorescence methods), and b) the measurement and meaning of light respiration, such a comparison would be troublesome at best, which is perhaps why we are unaware of a paper drawing such a comparison.**

**Overall, while we agree with the reviewer’s sentiment and find their questions intriguing, we believe that adding such \*potentially\* contentious information would distract from the main point of the manuscript. However, we believe that it would be worth revisiting the whole idea of activation energy as it is used in photosynthesis research in a future review/meta-analysis. In addressing Reviewer 3’s comments on the history of J1942, we did come across a paper by Sharpe and DeMichele (1977) that explain that while assuming a single controlling enzyme is not “literally correct, has great conceptual simplicity and general plausibility”. Although across such a broad range of temperatures, it seems likely that multiple enzymes would be rate limiting.**  
  
2.  A few sentences on future work needed beyond changing models would be helpful.  Comparing models is one thing, but comparing actual data, for example the photosynthetic temperature response and daily sums from whole-tree chamber experiments (e.g., Drake et al. (2019) and similar studies from the same group) might be useful.  
  
Drake JE, Tjoelker MG, Aspinwall MJ, Reich PB, Pfautsch S, Barton CVM (2019) The partitioning of gross primary production for young Eucalyptus tereticornis trees under experimental warming andaltered water availability. New Phytologist, doi: 10.1111/nph.15629.

**We have expanded the final paragraph of the discussion to include how the incorrect derivation (the Medlyn equation, M2002) could be problematic for both Earth system models as well as actual data collected using modelled photosynthetic temperature responses as suggested by Reviewer 2. While more extensive modelling would be required to determine discrepancies in previous work, we can postulate where these differences may lie (Lines 305-323).**

Reviewer 3’s Comments

Comments to the Author  
Thank you for inviting me to review paper: “A derivation error that affects carbon balance models exists in the current implementation of the Johnson et al. (1942) modified Arrhenius function”.  
  
This is an intriguing paper to review, suggesting that a large number of people have been implementing incorrect models of temperature response in global carbon cycle assessments. It has always been a worry of mine that certain key papers get repeatedly cited as “the ground truth”, and it is then possible for an error to become persistent. This sort of checking is to be welcomed, and of returning to early manuscripts.  
  
The working hypothesis of this paper is as follows. Equation (4) gives a standard temperature response function, and all expressed in absolute temperature. This equation is then rearranged in such a form as to allow understanding of the change relative to that of a temperature of +25oC. Ecological modellers often do this normalisation, to a common temperature. Working through various equation rearrangements, this eventually leads to Eqn (10). Equation (10) should be comparable to Eqn (3), except that the authors find a missing multiplicative equation term of (T/298.15).  
  
The missing term is found through various re-arrangement of the exponentials, from Eqn (4)-Eqn (10). However, it seems clear that the standalone “T” part of Eqn (4) will always be present, and cannot be convolved into the exponential parts. So the findings appear robust. However, do please recheck this algebra, as it is the cornerstone of the paper.

**We each independently re-checked the algebra and got the same result as presented in the manuscript.**  
  
The authors could try and track in a bit more detail the history of Eqn (3), to find when and how this extra multiplicative term might have been dropped. Considering, for instance, high latitudes, then temperatures of -5oC are often realised, and so this immediately demonstrates that this effect can be as large as a 10% error (i.e. 268/298 ~ 0.9). However, maybe some authors have simply regarded this still as a relatively small term. Can the authors, therefore, find other papers after year 1942, and where the T/298 term remains? To say the obvious, one quick way might be to see who has cited the 1942 paper during the 1950s-1990s (using one of the web peer-review paper indexing systems?).

**We traced the omitted term to 1979 by AE Hall. Hall (1979) built a model of photosynthesis using the J1942 temperature equation (though they only cite Sharpe and DeMichele, 1977, who use the correct version of J1942). Their reason for dropping the temperature term was: “In addition their [Sharpe & DeMichele 1977 – correct citation should be Johnson et al. 1942] linear T term was omitted because it has little influence on the function and would have prevented Eq. 22 [the M2002 equation] from approaching Eq. 21 [Arrhenius 1915 equation] in the limiting conditions of lower temperatures”. Thus part of our initial difficulty in tracing the error was that the equation has been wrongly attributed to Sharpe and DeMichele (1977) by particularly influential plant scientists.**

**We have added a section that reads: “We traced the origin of the dropped term to two papers: Hall (1979) and Farquhar et al. (1980). Both papers cite the M2002 equation as belonging to Sharpe and DeMichele (1977) when in fact it belongs to Johnson et al. (1942). In Hall (1979), the reasoning behind the dropped term is given as: “In addition their linear T term was omitted because it has little influence on the function and would have prevented Eq. 22 [the M2002 equation] from approaching Eq. 21 [equation 1 in the present study] in the limiting conditions of low temperatures” (Hall, 1979, page 305). Considering J1942, at 5 °C the error due to the dropped term would be ~278 K / 298 K = ~0.93, and at 45 °C would be 318 K / 298 K = ~1.07, so ~7% error at those temperatures. In context of measurement precision, such an assumption of “little influence” may have been reasonable at the time. However, the reason regarding the convergence of the two equation is simply tuning the model equations. Meanwhile, Farquhar et al. (1980) report that: “Eq. (36) is a simplified version of an equation developed by Sharpe and DeMichelle [sic] (1977) to describe the effect of temperature on enzyme inactivation” (Farquhar et al., 1980, page 84). In both cases, it appears that the intention was to simplify the equation, which in the process of simplifying, generated an error that was propagated for over 40 years.” Line 138-152.**  
  
A second aspect the authors might like to consider is returning to the reasoning behind how Johnson et al (1942) built the Equation (4). To my eye, it looks as if their intention is to expect reactions to be broadly linearly increasing in T, but at higher temperatures this saturates. Hence Johnson et al use the exponential terms to bring in that saturation. I did try to download the 1942 paper, but frustratingly under COVID19 lockdown, I cannot access all the journals from home as I can from my lab.

**Unfortunately, this paper is difficult to obtain (otherwise we would have written this manuscript back in 2016). Looking at the structure of the equation, the basic structure is a linear scaling with temperature multiplied by an exponential scaling with temperature. The saturation and reversible denaturation/inactivation of the enzyme is then described by the term containing Hd and ΔS which causes a saturation then reduction in the velocity of the reaction at high temperatures. The reasoning behind the equation structure was to simulate the reversible denaturation/inactivation of the enzyme. The equation describing the kinetics for J1942 is:**

**I1 = s \* k2 \* g \* [LH2] / 1 + K1**

**where s is a proportionality constant; k2 represents the equilibrium between the enzyme and substrate with the enzyme-bound substrate; g is related to the total number of enzyme molecules and the total number of molecules that combine with the enzyme in both the active and inactive states; [LH2] is the concentration of luciferin; K1 is the ratio of concentrations of active to inactive enzyme.**

**The authors note that the maximum is extremely sensitive to Hd and ΔS, while the curves are too sharp at the maximum. They further suggest that this equation is too simple and would require additional equilibria to better match the data. As well, this equation was developed for luciferase rates across only a 10 C range of temperatures, which in some respects means it has not been appropriately tested for the range over which we are using it.**

**We have not explicitly addressed this in the manuscript – we prefer to stay focused on the fact that there is a derivation error that broadly affects the interpretation of biological temperature responses and modeling of carbon gain, including a large portion of the CMIP6 models (which are used by the IPCC for climate prediction). We do however, explain that the equation is meant to describe reversible denaturation/inactivation of the enzyme on line 92.**  
  
I would be very happy to see another version of this paper. In the meantime, maybe the authors could make a few small changes:  
  
(1)     Please place more focus on the implications of the missing equation term, and make sure these appear in the first diagram i.e. Figure 1. This will then relate the bulk of the paper better to the title.

**We have rearranged the figures, presenting the environmental data now as Figure 3, and inserted the phrase “see Impacts on modelled net carbon balance for environmental data” (Line 213) to allow reordering of the figures. By including the new Table 1 as suggested by Reviewer 1, we can now better show the implications of the missing term for modeling photosynthesis – it impacts 17 of the 40 models used in CMIP6. This impact, and the effect on modelled carbon balance are what we seek to emphasize here.**  
(2)     Please go back through the literature to find, if possible, where the term is first dropped.

**Done. See earlier comment.**  
(3)     Where the term is dropped, see if this is because those authors believe it to have little variation in T, and so can be regarded as roughly unity.

**Done, see earlier comment. The reviewer’s line of thinking about little variation in T was correct.**  
(4)     See if the original derivation is based on a linearly-increasing response to T, with the exponentials used to “flatten off” the curve at high temperatures.

**Looking at the original formulation, it is a linearly-increasing response to temperature multiplied by an exponentially-increasing response to temperature, with exponentials to reduce the curve (not just flatten off) at high temperatures. The original formulation is meant to explicitly account for high temperature declines in biological reaction velocities.**  
(5)     Do check again all algebra.

**We have each independently re-checked the algebra and obtained the same solutions.**  
(6)     I appreciate the implications are expressed in terms of the carbon cycle, but I would place as much emphasis on the fundamental finding of the Eqn (10) versus Eqn (3) differences. See point (1) above.

**We appreciate the reviewer’s preferred emphasis, however we prefer to focus on the modeling implications of the missing term and the impact on our scientific community. By rearranging the figures, there is now more emphasis on the impact of the missing term for fitting photosynthetic temperature responses, and believe that the first few sentences in our discussion already places sufficient emphasis on this (both Figures 1 and 2 address the fundamental finding of the paper). We did add an additional clause on line 280 to point out that despite the derivation error, fitted response curves are visually similar.**

Smaller things  
  
The title is very long!

**We agree that the title is long, however we want a descriptive title that conveys the main point of the manuscript. We have removed the citation within the title, shortening it somewhat.**  
  
To allow reproducibility of the direct temperature responses – rather than onward implications for the global carbon cycle – then please give the numerical values of each parameter in Eqns (4)-(10). For instance, line 96 gives the value for R but not ΔH. Sorry if they are tucked somewhere else in the paper. Alternatively, Table 1 could be expanded beyond carbon cycle parameters. I realise these parameters will be common knowledge to those from the plant ecology community, but often it is physicists or mathematicians who code Earth System Models.

**In our modeling, we used over 400 values for each of the temperature response parameters as these are the parameters that become changed by swapping M2002 and J1942. In the accompanying R package, we include a .csv file with all the temperature response parameters used in the modeling. Unfortunately, it would be rather overwhelming and clunky to include all these numbers within the manuscript itself. Now however, we include the parameters for M2002 and J1942 in Figure 1 (formerly Figure 2).**  
  
This is likely for the typesetters. But given this is a  highly mathematical paper (and with some equation terms having “fractions over fractions”), then I hope that due consideration will be given to ensuring that adequate space is given to the equations, so they are clear. In other words, the font (e.g. in Eqn(7)) should be prevented from becoming too small.

**While the reviewer is likely correct on this being for the typesetters, we have purposefully increased the font size of the equations in the manuscript.**  
  
As above, I would maybe change the order of the figures, or their format. The most important part of this paper is illustrating that Eqn (10) is different to Eqn (3). This should be presented in Figure 1 in my view (not in the panels of Figure 2), as this follows the order of the paper in a more logical way.

**See our response to Reviewer 3 comment 1 above.**  
  
The descriptions around the transitions between how the authors get from Eqn (4) to Eqn (10) could be better. For instance, “Harmonizing the notation scheme to that typically used in plant ecophysiology”. Much better would be describing the parameters that are changed in name, or clustered together – and giving references throughout.

**We have made some modifications to the transitions between Eqn 4 and Eqn 10 to mention specific parameters when relevant.**  
  
Where numerical values are mixed with variable names, then the standard notation would be to either (1) put the numerical value first, or (2) use a “x” symbol. So, for instance, Eqn (8), first fraction in brackets, the denominator as either “298.15 RT” or “RT x 298.15”.

**We agree and have made this change throughout (e.g. Table 2).**

**REFERENCES**

**Farquhar et al. 1980. A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. Planta 149:78-90**

**Hall AE. 1979. A model of leaf photosynthesis and respiration for predicting carbon dioxide assimilation in different environments. Oecologia 43:299-316.**

**Sharpe PJH, DeMichele DW. 1977. Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64:649-670.**

**Sharwood, Robert E., et al. "Variation in response of C 3 and C 4 Paniceae Rubisco to temperature provides opportunities for improving C 3-photosynthesis." *Nat Plants* 2 (2016): 16186.**