

## ***Interactive comment on “JULES-CN: a coupled terrestrial Carbon-Nitrogen Scheme (JULES vn5.1)” by Andrew J. Wiltshire et al.***

### **Anonymous Referee #3**

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This manuscript explains the N cycle in the JULES-CN model which forms the land component of the UKESM. Simulations from the UKESM have contributed to the CMIP6 effort. The N cycle component of JULES, as explained, here is very simple compared to existing models out there. This is completely acceptable as long as it is clarified that the model parameterizations are simple, their limitations acknowledged, and the implications discussed. I am afraid, however, that the manuscript doesn't appear to do so and in my mind requires substantial work to address this and other concerns I raise below.

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## 1 Major comments

I have several major concerns.

1. It is well known that leaf N content is related to its photosynthesis capacity (Field and Mooney, 1986). When CO<sub>2</sub> increases, photosynthesis increases but this rate of increase is slowed if enough N is not available. This process is referred to as photosynthesis downregulation (McGuire et al., 1995). So, it is clear then, that N limitation acts on photosynthesis and thus on the gross primary production (GPP) flux. However, the approach used in the manuscript, in contrast, reduces the NPP (without adjusting the GPP) which is equivalent to reducing carbon use efficiency (CUE = NPP/GPP). Since there is no biological justification for this provided, I am struggling to understand the reasoning behind this. Also, if that framework is still used, TRIFFID models  $V_{cmax}$  as a function of leaf N content (eqn. 51 in Cox 2001) so it makes sense to adjust  $V_{cmax}$ .

Related to this concern, is the fact, that I am not able to find in the manuscript in detail how this reduction in NPP is implemented or how it results and because of the interaction of which processes. Unless I missed it, the only reference to this important process is made on line 78 as "... and then reducing plant net carbon gain to match available nutrients".

It is well known that current observation-based CUE is around 0.5. This is also seen in Figure 10. The CUE for the JULES-CN model is lower than that for the JULES-C model because that's how JULES-CN is designed - to lower NPP and hence CUE as CO<sub>2</sub> increases and N supply can't keep up. I am wondering what happens in a future simulation for RCP 8.5 scenario. Will your CUE drop down to something like 0.25 by year 2100 which seems totally unrealistic? This will be one implication of your model design since you have chosen to reduce NPP and not GPP.

2. The second big assumption in the model is that of fixed C:N ratios of plant tissues. The implications of this assumption are not discussed. Since C:N ratio of plants varies in space (as indicated by different values of  $n_{l0}$  in Table 1) this indicates their ability to adapt to different environmental conditions in space. Assuming, plants can do the same in time as CO<sub>2</sub> increases doesn't this imply that the assumption of fixed C:N is too strong and your model will limit NPP perhaps more excessively than it in the real world (with the caveat that in the real world GPP is constrained).
3. In context of model evaluation, it would have been extremely helpful to include a simulation in which N deposition is turned off. This simulation would have allowed to see if the effect of N deposition is indeed to increase NPP as would be intuitively expected.

In addition, the TRENDY model simulation S2 doesn't take into account land use change and the fertilization of crops. Crop fertilization is a major source of leaching and gaseous emissions of N<sub>2</sub>O and NO<sub>x</sub>. I am wondering if this is the possible reason that the simulated leaching in Figure 4 is so low compared to other estimates.

Also, does the model simulate the realistic sign of response when driven with climate forcing only.

Typically, a model's response to various forcings allows to see at least if the sign of the response is consistent with expectations.

4. I realize that there are very few observation-based estimates available for N related pools and fluxes. However, still there are plenty of quasi-observation and model based estimates against which model results could have been compared. For example, in Figure 4 there are no quasi-observed or model estimates for several quantities. Model estimates are, however, available for immobilization and mineralization (von Bloh et al. 2018), plant N uptake (Zaehle et al. 2010; Xu-Ri

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and Prentice, 2008; Wania et al., 2012), and inorganic N mass (von Bloh et al. 2018; Xu-Ri and Prentice, 2008; Wania et al., 2012). These estimates will allow to put your model results in some context.

5. Model parameterizations are not compared to other models, and the conceptual basis of parameterizations and their implications, are not discussed (as mentioned above for the choice to reduce NPP and use fixed C:N ratios) .

For example, biological nitrogen fixation (BNF) is modelled as a straight-forward function of NPP. This is okay but the manuscript doesn't note that meta-analysis studies have found that BNF increases with increasing CO<sub>2</sub> (Liang et al., 2016) but decreases with increasing N deposition and fertilizer application (Ochoa-Hueso et al., 2013) both of which apparently result in increase in NPP. In addition, BNF is typically higher over agricultural areas.

Similarly, all gaseous losses are expressed using  $N_{turnover}$  but in nature there are several pathways using which gaseous losses occur.  $N_2O$  and  $NO_x$  losses occur during nitrification (via nitrifier denitrification) and  $N_2$ ,  $N_2O$ , and  $NO_x$  losses occur during denitrification.

It would be scientifically beneficial for the manuscript, and for a reader, if simplifications made are clearly highlighted and their limitations discussed, because then it is possible to interpret the model results in light of these limitations.

6. The majority of the results shown in the manuscript focus on the ability of the new model to reproduce all the aspects of the C cycle as the previous model did. As a result, the N cycle module is not evaluated rigorously. The manuscript doesn't report N demand, how it changes over time, what part of the N demand is not met, what part of N demand due to increasing CO<sub>2</sub> is met by N deposition, time series of mineral N pool, time series of plant N uptake, time series of C:N ratio of whole plant and other plant components, and geographical distribution of simulated C:N ratios (even though I realize they are specified). Since this is the

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first time JULES' N cycle component is being published it is reasonable to expect that such a manuscript will rigorously assess the new N cycle module.

7. There is no mention of phosphorus cycle at all. It is well known that in the tropics phosphorus limits photosynthesis and not nitrogen. How is this accounted for? My guess is this is somehow built into the  $V_{cmax}$  rates which are a function of leaf N content (eqn. 51 in Cox 2001). If the model can reproduce correct zonal distribution of GPP it must take phosphorus limitation in the tropics somehow into account.
8. Finally, the lack of units, the lack of rate change equations for several pools, and unclear statements make it difficult to understand the model parameterizations as noted below in minor comments. In its current form, there is no way a reader can fully understand and reproduce the parameterizations reported here in some other model.

## 2 Minor comments

9. Abstract, line 8, "It represents all the key terrestrial nitrogen processes in an efficient way.". The word "efficient" here is misleading.
10. Abstract, line 9, I find it extremely confusing that BNF is mentioned as an external input. BNF is how N enters the coupled vegetation and soil system. Consider the case, if we were to refer GPP as an external input since that's how C enters the coupled vegetation and soil system. N deposition and fertilizer, on the other hand, can be called external because they are not natural just like fossil fuel emissions. On page 2, in addition to BNF, leaching is also referred to as an external (loss). This also seems strange since on the carbon cycle side we don't refer to heterotrophic respiration or dissolved inorganic C in runoff as external losses.

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11. Page 2, line 34, "Internally organic N is lost ...". Here "internally", perhaps is much better described as "cycling of N within the coupled vegetation and soil system".
12. Page 2, line 36, "Both inorganic and organic nitrogen may become available for plant uptake". Since organic N uptake is very small and therefore not even modelled (including in your model) perhaps it would be better if this is clarified.
13. Page 2, line 39. "In a changing climate, rising atmospheric CO<sub>2</sub> drives **an increase in the terrestrial carbon cycle** and Gross Primary Productivity (GPP)." This is a vague sentence. What does "an increase in the terrestrial carbon cycle" means?
14. Page 2, line 56, " ... are between a reduction of 39 % and a slight increase of 1 % ...". Please consider rewording this sentence/phrase. It is somewhat hard to follow.
15. Page 3, line 65. " ... and a new managed land module ...". Please consider rewording to "and a new module for land management ...".
16. Page 3, lines 72-74. "This is achieved by extending the implicit representation of nitrogen in the existing dynamic vegetation and plant physiology modules TO ENABLE A MORE COMPREHENSIVE NITROGEN CYCLE WITHIN THE LAND SURFACE". Please consider deleting the text in capitals given N cycle framework used here is extremely simplified.
17. Page 3, Lines 74-75. "Nutrient limitation operates through two mechanisms; the available carbon for growth and spreading is reduced and the decomposition of litter carbon into the soil carbon is slowed". The word spreading at this point in the manuscript is unclear. Only after reading the rest of the manuscript it is clear that "spreading" means changes in the spatial extent of vegetation. Please consider using another phrase/word to replace "spreading".

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Please also consider not using the phrase "decomposition of litter carbon into the soil carbon" here and elsewhere. Technically litter doesn't decomposes into soil carbon. As litter decomposes it releases CO<sub>2</sub> and the dead organic matter is broken into smaller more recalcitrant materials, which the models consider as soil carbon. In reality, of course, there is a continuum.

18. Page 4, lines 114-115. "As standard, JULES-C includes an implicit representation of nitrogen which has been extended to be fully interactive.". A sentence or two about how nutrient constraints on photosynthesis are implicitly modelled in JULES-C will be helpful.
19. Page 4, line 120. "The vegetation nitrogen component captures the nitrogen limitation **on the C stock**, and ...". As described here the N limitation acts on NPP which is a C flux and not on the C stock.
20. Page 4, last sentence, line 126. " ... it slows the rate of litter decomposition INTO SOIL ORGANIC MATTER." Please consider removing the phrase in capitals.
21. Page 5, lines 129-135. I felt, it is little too early to introduce the seven JULES-CN parameters given that at this point in the manuscript, the parameterization themselves haven't been introduced.  
  
Also on line 130, Does " ... the effective solubility of nitrogen", refers to solubility in water.
22. Section 3.1. It seems the model's roots are in fact fine roots (since  $R_c = L_c$  in eqn(3)), and coarse roots and stem are included in the  $W_c$  term. Please make this clear.
23. For eqn (1) please specify the units of all terms. I suspect these are KgC m<sup>-2</sup>.
24. For eqn (2) what are the units of  $\sigma_l$  and  $L_b$ .

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25. What are units of the individual terms in eqn (5) through (9) and the remaining equations.
26. Page 6, lines 160-178. This entire section is based on Figures 2 and 3 which form the backbone of specified C:N ratios and their variation with canopy height. It would be extremely helpful to know the basis of these relationships.
27. Page 6, lines 180-181. "Biological nitrogen fixation (BNF) is ASSUMED TO BE THE largest **natural** supplier of nitrogen to the terrestrial ecosystem". Consider removing the words in capitals and including the word in bold. Fertilizer application is the largest anthropogenic N flux and BNF is largest natural flux.
28. Page 6, line 181. "Following Cleveland et al. (1999), the nitrogen fixation is determined as a proportion of the net primary production before nitrogen limitation ( $NPP_{pot}$ )". This is incorrect. Cleveland et al. (1999) parameterized BNF as a function of actual evapotranspiration (AET) not NPP.

Also,  $NPP_{pot}$  is not defined anywhere close to this equation where it is introduced the first time. The first definition of  $NPP_{pot}$  occurs on page 9, line 242, as " $NPP_{pot}$  supplied to TRIFFID represents the potential amount of carbon that can be allocated to growth". Then a somewhat different definition occurs on page 19 which defines  $NPP_{pot}$  as the NPP when nitrogen is unlimited. Isn't  $NPP_{pot}$  just the NPP from the original framework without any reduction. I don't think, you do a calculation with unlimited N applied, per se.

In context of BNF, and eqn (9), the parameter  $\zeta$  is not listed in Table 1.

29. Page 7, Table 1. It would be extremely help if  $n_{l0}$  is inverted and written as  $\frac{1}{n_{l0}}$  in units of Kg C/Kg N so that the values are easily comparable to C:N ratios reported in literature.

Also,  $n_{l0}$  is listed twice in Table 1 and please consider rewording "Top leaf N concentration" to "N concentration at the canopy top".

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30. Page 7, lines 188-189. "However, in JULES-CN<sub>layered</sub> the vertical distribution of the **fixed** nitrogen in the soil **depends on the root distribution** ...". What does "fixed" refers to in this context?

Also, at this stage in the manuscript it is not clear what does "depends on root distribution" means?

31. Page 7, lines 201-203. "This distinction is inconsequential in the carbon only mode but is more critical when considering nitrogen interactions as the implication is that at all times the plant has enough nitrogen in reserve to maintain full leaf". From here on it becomes difficult to follow the logic used in the model. I am not able to understand what does "the plant has enough nitrogen in reserve to maintain full leaf" means?

32. Page 8, eqn. (10). I am confused here.  $L_b$  is introduced as a variable called **balanced leaf area index** but not explained what actually it means. In eqn (2), leaf C,  $L_C$  is a function of  $L_b$ . In equation (9), leaf area index (LAI) ( $L$ ) is also related to  $L_b$  through  $p$ . Somewhere here, there is the split of  $L_C$  into labile and non-labile (the one which determines the actual LAI). Did I get this correct? How are  $L$  in eqn. (9) and  $L_C$  in eqn. (2) related? Are they related through specific leaf area (SLA)?

33. All through up to this point in the manuscript, the rate change equations for the vegetation N pool are not presented. At this point in the manuscript, I am still unclear what "retranslocation" means. Is this the transfer of resorbed N from leaves before they are shed. If yes, to which plant components?

34. page 8, lines 251-216. "During leaf-off the labile component is the equivalent of the retranslocated leaf nitrogen **plus an additional store of nitrogen** in preparation for the following bud burst". This sentence introduces yet another pool. It would be really helpful if all the pools and their rate change equations are properly introduced.

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35. Page 8, line 29. "The mean canopy nitrogen content is described by ...". Please reword this to "The vertical distribution of leaf N content in the canopy is described by ...".
36. Page 9, line 235. "Canopy Leaf C:N ratios are resultingly 44% higher than top leaf ratios". I am unable to understand this. Does "canopy leaf C:N ratios" refers to mean canopy leaf C:N ratio or the vertical profile of C:N ratios along the canopy depth starting from the top.

If leaf N content in the leaves at the top of the canopy is higher and decreases exponentially, and if C content is uniform than it implies that C:N ratio of leaves is lower in the leaves at the top of the canopy and higher at the bottom. Integrating eqn (12) over LAI yields

$$\int_0^L n_{l0} \exp(-k_n z) dz = n_{l0} \frac{1}{k_n} (1 - \exp(-k_n L))$$

which implies that the mean C:N will depend on the LAI, L. So I am unclear where does the number 44% comes from.

37. Page 9. Section 3.1.4. The term  $\Lambda_{lc}$  in eqn. (13) is not defined and only when the reader reaches eqn. (21) it is clear what this term is. Similarly for  $\Lambda_{ln}$ .
38. Page 10. Line 263.  $\Lambda_{ln}$  is defined as the retranslocation of nitrogen from leaves and roots into the plant labile pool. I am not sure how does it relate to  $p$  in equation 10 which is also related to retranslocation.
39. Where is  $\Psi_c$  from equation (13) defined? Is this what  $\Psi$  is in eqn. (17)?
40. Page 10. Line 271. "The nitrogen available for growth is the total available nitrogen multiplied ...". Please reword this as "The nitrogen uptake used for plant growth is the total nitrogen uptake multiplied ...". I think, that's what is meant

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here. Available N sounds like the N available in the soil inorganic pool that can be potentially taken up by plants.

41. Page 10. Line 272. "Equations 13 and 15 are then solved by bisection such that the nitrogen uptake for growth ( $\Phi_g$ ) is less than or equal to the available nitrogen ...". Do you mean the bisection method to find root of an equation? This and remaining part of this paragraph is difficult to understand since there is no  $\Phi_g$  term in either equation (13) or (15).

In addition, since units of the various terms are not provided it is difficult to follow the equations on page 10.

42. Page 10, line 282. "... and  $N_v/C_v$  defines the whole plant C:N ratio ...". You mean  $C_v/N_v$ ?
43. In the absence of the competition module of the TRIFFID model properly described it is difficult for a reader to know what does "density-dependent litter production" and "density-dependent component for intra-PFT competition for space" means in Section 3.1.5. Please consider introducing this in a sentence or two.
44. Page 11, please define  $\Lambda_c$  and  $\Lambda_n$  in words explicitly where they are first introduced.  $\Lambda_c$  was introduced in equation (22) but not defined until next page near eqn. (28).
45. Page 11, lines 310-311. "The effect of nitrogen limitation on the litter carbon flux is captured in the excess carbon term  $\Psi_i$ ". Throughout the manuscript there is no expression for  $\Psi_i$  so it's difficult to understand it. I do understand based on what is written in the manuscript that it is the excess C that cannot be used. So it must be related to N uptake, allocation fractions for C, and specified C:N ratio of the three C pools.

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46. Page 12, line 339. " $\beta_R$  depends on soil texture". I don't think, this dependence can be too strong. Can you please mention the typical value of  $\beta_R$ .
47. The rate change equations for litter and soil C pools are helpful. Similar equations for vegetation C and N pools would be so helpful.
48. Page 13, line 349-350. "Input into the BIO and HUM nitrogen pools comes from the total immobilisation of inorganic nitrogen into organic nitrogen where  $I_{tot} = I_{DPM} + I_{RPM} + I_{BIO} + I_{HUM}$ ".  
 $I_{tot}$  is divided into BIO and HUM pools. Since BIO is the microbial pool shouldn't all immobilization end up there.
49. Page 13, eqn (33). Does the subscript  $i$  still refers to PFTs?
50. Page 13, line 365. "... the respired fraction ( $\beta_R$ ) and the C to N ratio of the destination pool ...". This is confusing since on line 339 ( $1-\beta_R$ ) was referred to as "the fraction of soil respiration that is emitted to the atmosphere".
51. Page 14, line 371. "... where  $i$  is one of RPM or DPM." Please use a different subscript here since you have used  $i$  previously to represent PFTs.
52. Pages 13 and 14. The  $F_N$  terms in eqn (36) limits the respiration of the DPM and RPM litter pools. So it is unclear to me why  $F_N$  would depend on  $I_{BIO}$  and  $I_{HUM}$  in eqn. (37). In this same equation, I am also unclear what is  $N_{avail}$  at this point in the manuscript. As with several other terms, the terms are introduced but their expressions are mentioned or the terms clarified much later which makes it very difficult to follow the logic. It is only further down in eqn. (51) that  $N_{avail}$  is clarified.

Also, in eqn. (37) what happens if  $D_{DPM}$  or  $D_{RPM}$  are negative? Is this possible, since mineralization can be more than immobilization?

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53. Page 14. Similarly in eqn. (39) can  $I_{tot}$  be more than  $M_{tot}$  making  $N_{gas}$  negative.
54. Page 15. Eqn.(41). Is  $f_{dpm}$  used here different from  $f_{DPM}$  used in eqn. (25).
55. Page 15. Lines 416-417."The litter inputs are distributed so that they decline exponentially with depth, with an e-folding depth of 0.2 m".  
With this parameterization can litter enter a soil layer even if there are no roots in that layer.
56. Page 15. Line 423. Please consider using "bulk" or "single layer" instead of "non-layered".
57. Please consider using another term for gaseous losses rather than turnover.
58. Page 16, Lines 433-434."Without this additional turnover available N may increase excessively, potentially due to excessive biological fixation **in regions that are generally unlimited**". What does "regions that are generally unlimited" means?
59. Page 16. Line 434-435. "In the current model configuration this parameter is set to 1.0 (360 day<sup>-1</sup>) such that the whole pool turns over once every model year".  
Do you mean 1.0 year<sup>-1</sup> which would translate to (1/360) day<sup>-1</sup> and not 360 day<sup>-1</sup>? Also, since the time step of the biogeochemistry is the same as for TRIFID (i.e. 10 days) there has to be  $\Delta T$  somewhere. And, I suspect, 360 is used and not 365 since the calendar year in the UKESM model is 360 days. Correct?
60. Page 16, line 436. "This results in an effective saturation limit of 0.002 KgN m<sup>-2</sup> ...". Not clear - saturation limit of what?
61. What are the units of  $\beta$  in eqn. (47). Just above eqn. (47)  $\beta$  is said to be assigned "a value of 0.1 based on sorption buffer coefficient of Ammonia although here it

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represents the sorption of all inorganic nitrogen species". Note here that typically only  $\text{NO}_3^-$  leaches into the runoff and not  $\text{NH}_4^+$  so please consider modifying this sentence.

62. Page 16. Eqn. (48). Isn't  $f_1$  simply the fraction of roots in each soil layer. And again,  $f_2$  is not defined or described here but further down in eqn. (53).
63. Page 16. Line 453. "where  $f_{root}(z)$  is the volumetric root fraction at a given depth". You mean "for a given soil layer" as opposed to "at a given depth". And, an  $i$  subscript seems to be missing here. Although, I wouldn't suggest using  $i$  which has been used for PFTs, DPM or RPM, and now soil layers. Very confusing!
64. Page 17, eqn. (50). Is the parameter  $\tau_{resp}$  tuned so that  $N_{turnover}$  is similar in the "bulk" and "layered" versions.
65. Page 17. Eqn (51). Assuming, the subscript  $i$  represents the PFT shouldn't there be (z) term here to indicate the nitrogen availability in each layer.
66. Page 17. Eqn (52). I am unable to follow eqn. (51). Looking at eqn. (51) the term in parantheses in eqn. (52) should be zero since  $f_{root,i} N_{in} = N_{avail,i}$  from eqn. (51).

The value/units of  $\gamma_{diff}$  is also confusing. I am not sure what  $100 [360 \text{ day}]^{-1}$  means.

67. Page 17, lines 471-474. "Any fixation goes directly into the available pool, and other fluxes are simply added according to the ratio of the available to total inorganic N pools at equilibrium (thus the available pool would always follow Equation 51 were it not for the fixation and uptake by plants)". I am sorry but I am unable to follow this sentence.

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68. Page 17. Eqn. (54). In the absence of its units, I am not sure if the term  $dz_n$  is a single variable or do you mean  $\Delta z_n$ . And, I have no clue, what  $z_n$  is at this point in the manuscript.
69. Page 17. Line 483. "... is then the sum of all nitrogen that leaves the soil by lateral runoff ...". Does the lateral runoff from each layer mean that JULES is capable of producing runoff based on slope of the ground? Please clarify what exactly lateral runoff means.
70. Page 18. Lines 501-502. "They were spun up by repeating the time period 1860-1870 ...". This is confusing. Please consider rewording as "The models were spun up by using the meteorological data for the period 1860-1870 repeatedly ..."
71. Page 19. Lines 522-524. "The main difference is the present-day NPP which is 12% higher in JULES-C than in JULES-CN. **This is a direct consequence of nitrogen limitation which restricts the ability of the plants to utilise all of the carbon**". No this is the direct consequence of JULES-CN reducing NPP. I don't think, it is necessary to spin this in a more biological way.
72. In Figure 4, it would be really useful to see separate estimates for mineralization and immobilization. In its current form, only net mineralization is reported.
73. Page 20. Lines 580-582. "This [CUE] represents the capacity of the plants to allocate carbon from photosynthesis to the terrestrial biomass". I don't think this sentence is entirely correct. Since CUE is the fraction of GPP converted to NPP, it is a measure of autotrophic respiration.
74. Page 20, line 582-583. "In the model nitrogen limitation restricts the ability of plants to allocate carbon and reduces the carbon use efficiency". Here again, the "restriction of ability of plants to allocate carbon" appears as if carbon is there but

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some how plants can not allocate it. In contrast, as JULES-CN is designed, there is simply less carbon to be allocated. I don't think, JULES' allocation module has been changed in JULES-CN to limit how much C flows to different components.

75. Page 21. Line 596. "... by structural changes in the vegetation in particular ...". Please clarify if structural changes refer to changes in vegetation height, LAI, and rooting depth.
76. Page 22. Lines 626-628. "There remains a significant underestimate of NEE in the years following the Pinatubo volcanic eruption ...". Please make it explicit in which year Pinatubo erupted since it's not marked in Figure 12.
77. Page 22. Line 646. Please change "tome" to "time".
78. Page 23. Line 656. "In this model, nitrogen limitation affects NPP and how the carbon is allocated ...". As mentioned above, I think, it's more appropriate to say **how much C is allocated** since the underlying C allocation module has not changed between JULES-C and JULES-CN.

### 3 References

1. Cox, P. (2001). Description of the "TRIFFID" Dynamic Global Vegetation Model. Met Office, Hadley Centre Technical 24.
2. Field, C. and Mooney, H.: The Photosynthesis-Nitrogen Relationship in Wild Plants, *Biol. Int.*, 13, 25–56, 1986.
3. Liang, J., Qi, X., Souza, L. and Luo, Y.: Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis, *Biogeosciences*, 13(9), 2689–2699, doi:10.5194/bg-13-2689-2016, 2016.



4. McGuire, A. D., Melillo, J. M. and Joyce, L. A.: The role of nitrogen in the response of forests net primary production to elevated atmospheric carbon dioxide, *Annual Reviews Ecol. Syst.*, 26(1), 473–503, doi:10.1146/annurev.es.26.110195.002353, 1995.
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