

We thank the reviewers for their helpful comments on the manuscript. Below we address their individual questions and comments and note where revisions occur in the marked-up version of the manuscript. Our responses are in blue, with the updates to the manuscript italicized. The relevant line numbers in the revised manuscript are provided in red.

In the marked-up manuscript, blue text denotes additions and deletions of text, and green text denotes text that was moved.

Reviewer 1

1. Line 160-165. What are the observational ranges for a_{wl} and a_{ws} . Are the adjusted values within observed ranges? How applicable are fixed values of these parameters for stands of different ages, and what are the implications for carbon accumulation in young vs old-growth forests?

Response:

The ratio of live sapwood/stem to wood (parameter a_{ws}) varies significantly with tree species: at least between 0.05 and 0.28 according to Friend et al. (1993), which corresponds to a_{ws} between 4 and 20. Our values of a_{ws} (10-13 for woody vegetation) are therefore well within the range of observations. Although we expect variations in a_{ws} and a_{wl} across tree species, these are ratios that are relatively invariant with tree size/age within tree species or functional types, consistent with allometric relationships (e.g. Niklas & Spatz, 2004) and “pipe model” relationships between leaf-area and stem-area (e.g. Ogawa, 2015).

We will add this context into the Methods section where the new values of a_{ws} and a_{wl} are given. This has been added, see lines 160-163.

2. Biomass from Ruesch and Gibbs (2008). Could you justify why you don’t use more up-to-date biomass products, eg GEOCARBON (Avitabile et al. 2016), https://www.wur.nl/en/Expertise-Services/Chair-groups/Environmental-Sciences/Laboratory-of-Geo-information-Science-and-Remote-Sensing/Research/Integrated-land-monitoring/Forest_Biomass.htm

Response:

The Ruesch and Gibbs (2008) biomass is an estimate of total carbon in above- and below-ground biomass, while GEOCARBON only covers aboveground biomass in forests. Therefore, Ruesch and Gibbs (2008) allows a more thorough comparison of the JULES outputs. However there is large variation in estimates of biomass, as was pointed out in Avitabile et al. (2016). We therefore also compared our biomass estimates to a dataset from Carvalhais et al. (2014) (Fig. 3c), which were derived using Saatchi et al. (2011) for the Tropics and Thurner et al. (2014) for boreal and temperate regions.

We will include some further context in the discussion addressing the uncertainty in global datasets of biomass. See lines 550-555.

3. Figure 1. What quantity is being mapped ? Is it area fraction? Please make it clear in the text and figure caption.

Response:

Figure 1 shows the fraction of vegetation types and bare soil in each grid cell. *We will update the text and the figure caption. This has been changed.*

4. L340. If the agricultural land is prescribed, how can the model under-estimate it?

Response: The fraction of land in a grid cell dedicated to agriculture is specified based on Hyde data set. We assume that only C3 and C4 grasses can grow on agricultural land, but if the simulated NPP is not sufficient to support vegetation, there will be bare soil instead. This is why the agricultural fraction can be underestimated. To compare with the ESA PFT distribution, we reduced the “observed” agricultural fraction on grid cells where the prescribed agricultural fraction is greater than the grasses in the grid cell. This is why the agricultural fraction can also be higher than indicated by ESA.

We will clarify these two points in the text. See Lines 385-392.

5. L. 435. “in agreement with the high bias in simulated NPP”. Please revise this stated agreement. High bias in NPP doesn’t necessarily give high NBP. It is the magnitude NPP, relative to that of heterotrophic respiration that dictates the magnitude of the land carbon sink, with the difference related to the different rates of change of these two fluxes.

Response: This is a good point. There are two points we should make here. First, the doubling of NBP was due to an increase in NPP not matched by an increase in heterotrophic respiration. Second, although simulated NBP in the 1980s was in between estimates from GCP and IPCC, the simulated NBP in the 2000s was higher than both constraints, indicating that either the increase in NPP was too large, or the response from Rh was too low. The high bias in NPP noted earlier in the paper supports the former, but this doesn’t rule out the possibility that Rh was undersensitive to climate and CO₂ over the period 1980-2009.

We will update the text with this information. See Lines 503-504 and 614-619.

6. Figure SM7: different colours or line-styles are needed to distinguish the two simulations.

Response: We will add colors to the lines in this Figure. Figure has been updated, also in updating the figure we found that an additional 200 years of spin up was performed with the CRUNCEPv6 climate, which we have added to SM Figure 7 (years 100-299 in the new figure were missing in the previous version). The rate of change of soil carbon is smoother with all of the data included (see response to final comment from Reviewer 2).

7. Can you explain why biomass in central Africa is well simulated (Fig. 3-4), but vegetation distribution is not (Fig 1).

Response: In Central Africa, the model simulates too many broadleaf trees and virtually no shrubs, although these are regions with large uncertainties in the ESA vegetation observations (Hartley et al. 2017). A similar bias is apparent in subtropical South America. In both regions (outside of the central tropical forests), fires suppress tree growth and this process is missing in the model. The overestimation of trees and underestimation of shrubs is also apparent in Figure 2. The spatial distribution of vegetation carbon is similar to observations (Fig. 3), but due to the extent of the broadleaf forests the total vegetation carbon in the Tropical Forest biome is higher than observed (Fig. 4).

We already mention the fact that this version of JULES does not have interactive fires (new lines 577-579), so we will add to this discussion as these are regions where we expect an improvement after representing the effects of fires. See lines 454-456, 557-560.

8. Satellite-based NPP. Please consider referencing uncertainty in this product, for example, satellite-based NPP datasets have large uncertainties in tropical regions (Cleveland et al. 2015), e.g. from saturation of the fraction of photosynthetically active radiation (FPAR) in high vegetation density areas.

Response: There are a few papers estimating the uncertainty in MODIS NPP in the Tropics, but unfortunately the product does not contain uncertainty estimates. There is approximately a 15% uncertainty in global estimates of NPP (Ito 2011). Also as the reviewer mentioned, there is large disagreement in NPP from inventories, satellites, and models in the tropics (Cleveland et al. 2015).

We will add some discussion in the paragraph describing NPP results (beginning at the top of page 19) about the uncertainty in this product to give some context to the apparently high NPP in JULES. See Lines 520-538.

Reviewer 2

- Line 148: Please refer to Table 2 already here.

Response:

We will correct this in the revised manuscript.

- Line 259: Could be written more clearly. Equilibrium vegetation mean $dv/dt = 0$ in eq (1), which directly yields eq. 17. Please use Sum symbol in eq. 17 (as done in eq 16), no need to keep eq 16 which is almost identical.

- To this point, it should be stressed that the disturbance parameters are tuned such that the equilibrium vegetation is OK. Therefore the relatively good results in fig 1 and 2 should not be too surprising. Please state this clearly also in the discussion. Are these disturbance parameters realistic? Any chance to evaluate them?

In response to the above two points:

We agree that Eq. 16 is not necessary, and we will correct Eq. 17. Also, we will update this text to make it clearer, and to better explain the process for selecting new values of the disturbance parameter.

Equation 17 was used to calculate a new γ for each PFT in each gridcell. We chose the new parameter value as the median value in grid cells with <50% agriculture (Lines 270-273). The simulated distribution of PFTs would be even more realistic if we used spatially varying values for γ , but part of the reason for the model not recreating observed distributions is because of the use of one global value per PFT. Also the calibration of γ was based on a simulation in equilibrium, while Figures 1 and 2 show distributions after the transient run, when vegetation fractions are not in equilibrium.

We will highlight these points in the revised text.

We will also update this text to better describe what the disturbance parameters are representing: The parameter represents several missing processes in JULES related to disturbance-induced mortality (such as fires, pests, and windthrow). The value of the parameter would be difficult to evaluate since it represents several processes, although the general values give an estimate of turnover rates for the PFTs. As such, the numbers do make sense: there are low turnover rates for trees, high turnover rates for grasses, and moderate rates for shrubs.

The above points are addressed in the updated text in Section 3.2, particularly Lines 282-287, 294-301.

- Line 327: Small differences between the results with CRUNCEP and HadGEM-ES climate. Is this due to the fact the the HadGEM-ES climate is so realistic, or does this suggest that JULES is not very sensitive to climate differences for some reason, except for some specific PFTs mentioned explicitly?

Response: We plan to add a figure to the SM comparing the temperature and precipitation of the CRUNCEP and HadGEM2-ES climates.

The HadGEM2-ES does broadly represent the present climate very well, but there are biases in the model that have an impact on the vegetation distribution. Mapping the climates will enable us to link differences in simulated vegetation fraction to differences in the two driving climates.

We have added Figure 3 showing the relationship between simulated and observed fractions of tree coverage per biome and biome-average climate variables (temperature, precipitation, specific humidity and shortwave radiation). Also see new text at Lines 344-346, 370-379, 415-416. We also added supplemental Figure SM8 to show precipitation, temperature and humidity in each biome.

- Figure 2: Hard to evaluate the differences between the different model configurations with the naked eye. Could one add an error statistic for each of the biomes and model configs? You could consider adding the PFT names (that is, spelling out their acronyms) in the legend, might be helpful.

Response: Thank you for this suggestion – we will include the full names of the PFTs in the legend. Also, the error metric was calculated per PFT (Eq. 15), but it could just as easily be calculated per biome. We will do this and add that information to the plot.

We have updated Figure 2 and added the equation for the bias per biome (Eq. 16). There is new text, see lines 229-236 for description of the new statistic and 425-430 for the results.

- Carbon spinup: The carbon spinup figure in the supplement shows that some PFTs are quite far from equilibrium at the end of the accelerated spinup, and that large instantaneous adjustments follow after that, which seem to have consequences over the whole transient period. Please discuss potential impacts on the soil carbon evaluation and discuss briefly. First we point out that the figure is showing soil carbon in the four soil pools, not PFTs. But the reviewer is right in pointing out some questionable behaviour in this figure. *We will double-check the plotting routine for errors.* The turnover times for the RPM, biomass, and humus pools were increased during the accelerated decomposition phase. To create this figure, the soil carbon pools were multiplied by the rescale factors for each pool (Table 3),

but it's possible we did not apply the correct scaling factors. The pool sizes should be smaller during the accelerated decomposition phase, instead of being larger as they are in the RPM and Biomass pool for CRUNCEP.

We found that an additional 200 years of spin up was performed with the CRUNCEPv6 climate, which we have added to SM Figure 7 (years 100-299 in the new figure were missing in the previous version). The rate of change of soil carbon is smoother with all of the data included, except for the RPM pool which decreased by ~20 PgC at the end of the accelerated phase. The decrease occurred with both climate forcings, and we are confident it's not a mistake in the plotting. The RPM pool readjusted quickly, and it changed by at most 1 PgC over the last 100 years of the spin up. The figure has been updated in the SM, and we have clarified these points in the new manuscript (Section 3.3, particularly lines 334-339).

Vegetation distribution and terrestrial carbon cycle in a carbon-cycle configuration of JULES4.6 with new plant functional types

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Abstract. Dynamic global vegetation models (DGVMs) are used for studying historical and future changes to vegetation and the terrestrial carbon cycle. JULES (the Joint UK Land Environment Simulator) represents the land surface in the Hadley Centre climate models and in the UK Earth System Model. Recently the number of plant functional types (PFTs) in JULES were expanded from 5 to 9 to better represent functional diversity in global ecosystems. Here we introduce a more mechanistic representation of vegetation dynamics in TRIFFID, the dynamic vegetation component of JULES, that allows for any number of PFTs to compete based solely on their height, removing the previous hardwired dominance hierarchy where dominant types are assumed to outcompete subdominant types.

With the new set of 9 PFTs, JULES is able to more accurately reproduce global vegetation distribution compared to the former 5 PFT version. Improvements include the coverage of trees

within tropical and boreal forests, and a reduction in shrubs, which dominated at high latitudes. We show that JULES is able to realistically represent several aspects of the global carbon cycle. The simulated gross primary productivity (GPP) is within the range of observations, but simulated net primary productivity (NPP) is slightly too high. GPP in JULES from 1982-2011 ~~is was~~ 133 PgC yr⁻¹, compared to observation-based estimates between 123±8 (over the same time period) and 150-175 PgC yr⁻¹. NPP from 2000-2013 ~~is was~~ 72 PgC yr⁻¹, compared to satellite-derived NPP of 55 PgC yr⁻¹ over the same period and independent estimates of 56.2±14.3 PgC yr⁻¹. The simulated carbon stored in vegetation is 542 PgC, compared to an observation-based range of 400-600 PgC. Soil carbon is much lower (1422 PgC) than estimates from measurements (>2400 PgC), with large underestimations of soil carbon in the tropical and boreal forests.

We also examined some aspects of the historical terrestrial carbon sink as simulated by JULES. Between the 1900s and 2000s, increased atmospheric carbon dioxide levels enhanced vegetation productivity and litter inputs into the soils, while land-use change removed vegetation and reduced soil carbon. The result ~~is was~~ a simulated increase in soil carbon of 57 PgC but a decrease in vegetation carbon ~~by~~ of 98 PgC. ~~The total simulated loss of soil and vegetation carbon of 14 and 124, respectively,~~ due to land-use change ~~is~~ 138 PgC from 1900-2009, ~~compared to a recent observationally-constrained estimate of 155±50 PgC from 1901-2012.~~ The simulated land carbon sink ~~is was~~ -2.0±1.0 PgC yr⁻¹ from 2000-2009, in close agreement to estimates from the IPCC and Global Carbon Project.

1. Introduction

Dynamic global vegetation models (DGVMs) are used for predicting changes in vegetation distribution and carbon stored in the terrestrial biosphere (Prentice et al., 2007; Fisher et al., 2014). When coupled to climate models, these tools enable the study of interactions between climate change, land use patterns, and the terrestrial carbon cycle. Typically, DGVMs either group the

world's vegetation types into plant functional types (PFTs), or aggregate vegetation sharing a common biogeography into biomes (Woodward, 1987; Running and Gower, 1991; Prentice et al., 1992). A move towards a PFT approach recognized the differential response of plant function to rapid future climate change (Foley et al., 1996; Sitch et al., 2003). However, due to data limitations these models were handicapped in the number of PFTs they could define and differentiate.

JULES (Best et al., 2011; Clark et al., 2011) is a DGVM that represents the land surface in the UK Hadley Centre family of models (e.g. the UK Earth System Model in the 6th phase of the Coupled Model Intercomparison Project, CMIP6, and the HadGEM2 models in CMIP3 and CMIP5). Within JULES, TRIFFID (Top-down representation of Interaction of Foliage and Flora Including Dynamics; Cox, 2001) predicts changes in the carbon content of vegetation and soils, and vegetation competition. Since its creation in the late 1990's, competition in TRIFFID was limited to between five PFTs (broadleaf trees, needle-leaf trees, C3 and C4 grasses, and shrubs). Under this approach, each PFT competed with other PFTs based on a prescribed hierarchy, where dominant PFTs were assumed to outcompete subdominant PFTs. The proliferation of new ecological data over the past decade has provided the opportunity to improve TRIFFID and the entire JULES model on a range of scales: for example, the TRY database stores detailed information on plant traits that are important for the processes of photosynthesis and respiration (Harper et al., 2016), while on the global-scale new vegetation maps enable improved analysis of predicted plant distributions (e.g. (Poulter et al., 2015). Exploitation of these new datasets allow a more detailed representation of vegetation distribution and the terrestrial carbon cycle, and improve the biophysical characterization of the land-surface in climate models (e.g. albedo implications of deciduous versus evergreen phenology in boreal forests).

The physiology of JULES was recently updated to include the following leaf traits: leaf mass per unit area, leaf nitrogen per unit mass, and leaf lifespan. An iterative process of development and

evaluation with JULES resulted in an improved representation of gross and net primary productivity (GPP and NPP, respectively) based on an expanded set of PFTs (Harper et al., 2016). The new PFTs were also used in the development and evaluation of a new fire module in JULES (Interactive Fire and Emission algorithm for Natural environments, or INFERNO; Mangeon et al., 2016). However, given the primary focus on improved physiology, the Harper et al. (2016) study adopted a prescribed vegetation distribution based on satellite data. Here we present developments in the representation of vegetation dynamics in TRIFFID and include an evaluation of the expanded set of PFTs on simulated global vegetation distribution, and associated global carbon stocks and fluxes. This paper aims to demonstrate the overall performance of the new version of JULES in offline (not coupled to a climate model) simulations compared to both independent data sources and a previous version of the model.

2. Methods

2.1 JULES and TRIFFID

JULES simulates the processes of photosynthesis, autotrophic and heterotrophic respiration, and calculates the turbulent exchange of CO₂, heat, water, and momentum between the land surface and the atmosphere (Cox et al., 1998; Best et al., 2011; Clark et al., 2011). Vegetation dynamics are simulated by TRIFFID. Recently, new PFTs were added to JULES (Harper et al., 2016) (Table 1), which required updates to the TRIFFID competition scheme, described below. In this paper, we compare two versions of JULES: JULES-C1 and JULES-C2 based on JULES version 4.6. The former is a configuration of JULES with five PFTs as described in Harper et al. (2016) (called JULES5 in that paper) and as used in the TRENDY multi-DGVM synthesis project (Sitch et al., 2015). The latter (JULES-C2) is the new version, with 9PFTs and vegetation dynamics and updates described in Sections 2.2-2.3.

2.2 Vegetation dynamics and new height-based competition

Within TRIFFID, carbon acquired through NPP is allocated to either spreading (in other words
 105 increasing fractional coverage of a PFT in a grid cell) or growth (increasing height). The time
 evolution of fractional coverage of each PFT i (v_i) is calculated as:

$$C_{V_i} \frac{dv_i}{dt} = \lambda_i \Pi_i v_* (1 - \sum_j c_{ij} v_j) - \gamma_v v_* C_{V_i} \quad (1)$$

where C_V is the vegetation carbon (kgC m^{-2}), Π is the accumulated NPP between calls to TRIFFID
 ($\text{kgC m}^{-2} (360 \text{ d})^{-1}$), v_* is the maximum of the actual fraction and a “seeding fraction” (0.01), and γ_v
 110 is a PFT dependent parameter representing large-scale disturbance ($360 \text{ d})^{-1}$. In the present study,
 TRIFFID ran on a daily time step. The fraction of NPP allocated to spreading, λ , is a function of the
 balanced LAI, L_{bal} , which is the seasonal maximum of LAI based on allometric relationships (Cox,
 2001):

$$\lambda = \begin{cases} 1 & \text{for } L_{\text{bal}} > L_{\text{max}} \\ \frac{L_{\text{bal}} - L_{\text{min}}}{L_{\text{max}} - L_{\text{min}}} & \text{for } L_{\text{min}} < L_{\text{bal}} \leq L_{\text{max}} \\ 0 & \text{for } L_{\text{bal}} \leq L_{\text{min}} \end{cases} \quad (2)$$

115 and the fraction allocated to growth is $(1-\lambda)$. The PFT-dependent parameters L_{max} and L_{min}
 determine the balanced LAI at which plants allocate 100% of NPP toward expanding PFT coverage
 (spreading: $L_{\text{bal}} \geq L_{\text{max}}$) or 100% toward vertical plant growth ($L_{\text{bal}} < L_{\text{min}}$).

Competition for space in the grid cell between PFT i and the other PFTs is represented by the
 120 matrix c_{ij} , which represents a dominance hierarchy where height is the most important factor as it
 determines access to light. Effectively, the $(1-\sum_j c_{ij} v_j)$ term in Eq. 1 is the space available to PFT i . In
 the original version of TRIFFID, trees were assumed to dominate shrubs, and shrubs were assumed
 to dominate grasses (Cox, 2001). Within tree (broadleaf and needle-leaf) and grass (C_3 and C_4)
 PFTs, there was co-competition and c_{ij} was calculated as a function of vegetation height for the two
 125 competing PFTs:

$$c_{ij} = \frac{1}{1 + \exp\left[20 \frac{h_i - h_j}{h_i + h_j}\right]} \quad (3)$$

We made two changes to the original TRIFFID: first we removed the hard-wired dominance hierarchy (trees>shrubs>grasses) to allow for a generic number of PFTs. The dominance hierarchy is now completely height-based, so that the tallest PFTs get the first opportunity to take up space in a grid cell. Second we removed co-competition, so that c_{ij} is either 1 or 0. This simplifies the equilibrium solution for vegetation coverage (Section 3.2), as will be explained later. When PFT i is dominant, $c_{ij} = 0$ and PFT i is not affected by PFT j ; when type j is dominant, $c_{ij} = 1$ and PFT i does not have access to the space occupied by PFT j (v_j).

2.3 Updated parameters for JULES-C2

Although the version of JULES described in this paper is similar to that described previously by Harper et al. (2016), there are four differences, which are summarized here. ~~The impacts of the new allometric parameters and introduction of the geographic variation of soil clay fraction are described in Section 3.2.~~ Impacts of the new equations for leaf, root, and stem nitrogen are discussed in detail in the Supplemental Material.

2.3.1 Allometric parameters

At the end of a TRIFFID timestep, the portion of NPP allocated toward growth increases the carbon content of leaves, roots, and wood. Both leaf and root carbon is linear with the balanced LAI, while total wood carbon (C_{wood}) is proportional to L_{bal} based on the power law (Enquist et al., 1998):

$$C_{wood} = a_{wl} * L_{bal}^{b_{wl}} \quad (4)$$

The parameter a_{wl} is a PFT-dependent coefficient relating wood to leaf carbon (units of kgC m^{-2} per unit LAI), and b_{wl} is a parameter equal to $5/3$ (Cox, 2001). Previously, a_{wl} was 0.65 for trees, 0.005 for grasses, and 0.10 for shrubs. After carbon pools are updated, canopy height is calculated from Eq. (5):

$$h = \frac{C_{wood}}{a_{ws}\eta_{sl}} * \left(\frac{a_{wl}}{C_{wood}} \right)^{1/b_{wl}} \quad (5)$$

The derivation of Eq. (5) is based on the assumption that total wood carbon is proportional to carbon in respiring stemwood (S), which itself is proportional to leaf area and canopy height (h) based on the live stemwood coefficient, η_{sl} ($= 0.01 \text{ kgC m}^{-1} (\text{m}^2 \text{ leaf})^{-1}$, derived from Friend et al. (1993)):

$$C_{wood} = a_{ws} S \quad (6)$$

$$S = \eta_{sl} h * L_b \quad (7)$$

In Eq. (6), a_{ws} is the ratio of total wood carbon to respiring stem carbon, it was previously 10.0 for trees and shrubs and 1.0 for grasses, but this varies significantly with tree species: at least between 5 and 20 according to Friend et al. (1993). These ratios are relatively invariant with tree size and age within tree species or functional types, consistent with allometric relationships (e.g. Niklas and Spatz, 2004) and “pipe model” relationships between leaf-area and stem-area (e.g. Ogawa, 2015).

As shown in the Results, there was a low vegetation carbon bias in JULES-C1, especially in regions dominated by broadleaf trees and shrubs. To increase vegetation carbon in areas where the model was lower than observed, we increased a_{wl} and a_{ws} , while keeping their ratio constant, to the values given in Table 2. In order to address the bias, we modified the allometric parameters a_{wl} and a_{ws} in the model. Changing a_{wl} alone would affect the competitiveness of a PFT because it also affects plant height, h .

2.3.2 Soil respiration

JULES soil carbon is modelled with the Roth-C carbon model (Jenkinson, 1990; Coleman and Jenkinson, 2014). There are four pools: decomposable plant material (DPM), resistant plant material (RPM), microbial biomass (BIO), and humus (HUM). Respiration from each pool is calculated based on soil temperature (T_{soil}), moisture content (s), vegetation cover (v), and a pool-dependent turnover rate (κ_i):

$$R_i = \kappa_i * C_i * F_T(T_{soil}) * F_s(s) * F_v(v) \quad (8)$$

The turnover rates for the four soil carbon pools are 10 yr^{-1} for DPM, 0.3 yr^{-1} for RPM, 0.66 yr^{-1} for

microbial biomass, and 0.02 yr^{-1} for humus (Coleman and Jenkinson, 2014). These are based on experiments on the decomposition of ^{14}C labelled ryegrass over a 10-year period under field conditions ($\sim 9.3^\circ\text{C}$ and $> 20 \text{ mm}$ of water) (Jenkinson, 1990). For both JULES-C1 and JULES-C2 in this paper, a Q_{10} formulation was used for F_T (Eq. 65 in Clark et al., 2011). However, only a fraction of respired carbon actually escapes to the atmosphere to represent the protective effect of small particles:

$$R_{\text{soil} \rightarrow \text{atmos}} = (1 - \beta_R) \sum_{i=1}^{\text{scpool}} R_i \quad (9)$$

where

$$\beta_R = 1/[4.0895 + 2.672 * e^{-0.0786 * \text{Clayfrac}}] \quad (10)$$

Until version 4.6, JULES used a global clay fraction of 0.23 for this equation, which was based on the clay content at the site where the Roth-C model was calibrated. Now JULES uses a geographical variation of clay content based on the clay ancillary from the HadGEM2-ES CMIP5 simulations. All versions of the model presented in this study implement the global maps of clay.

2.3.3 Root and Stem Nitrogen

Third, new equations for root and stem nitrogen content (N_{root} and N_{stem} , respectively) were added using updated data from the TRY database (Harper et al., 2016):

$$N_{\text{root}} = n_r * C_m * LMA * L_{\text{bal}} \quad (11)$$

$$N_{\text{stem}} = \eta_{sl} * h * L_{\text{bal}} * n_{sw} \left[\frac{1}{a_{ws}} + \left(1 - \frac{1}{a_{ws}} \right) * hw_{sw} \right] \quad (12)$$

where C_m is the ratio of carbon per unit biomass ($=0.4$), LMA is the leaf mass per unit area for top of the canopy leaves, n_r is the ratio of root N to root C, n_{sw} is the ratio of stemwood N to stem C, and hw_{sw} is the ratio of heartwood N to stemwood N. The latter is set to 0.5 based on a recommended range of 0.4-0.6 (Hillis, 1987). Parameters n_r and n_{sw} were calculated from the TRY database (Table 2).

2.3.4 Leaf nitrogen distribution

Fourth, updates were made to the parameter that characterizes the vertical distribution of leaf N through the canopy. Although these updates do not affect radiation interception through the canopy, they are referred to in the code as canopy radiation model 6 (“CRM6”). JULES splits the canopy into 10 layers of equal LAI increment. In CRM6, leaf N declines exponentially through the canopy, so that for canopy layer i , the leaf N content (N_{leaf} , kg N m⁻²) is:

$$N_{\text{leaf}_i} = N_m * LMA * e^{-k_{nl} * Li} \quad (13)$$

where N_m is leaf nitrogen per unit mass at the top of the canopy and k_{nl} is a decay coefficient (=0.20). In JULES-C2 we update the value of k_{nl} (Lloyd et al., 2010) and include the explicit term for LAI (L) in Eq. (13). The mean leaf N content is:

$$\overline{N_{\text{leaf}}} = \frac{N_m * LMA * (1 - e^{-k_{nl} * L})}{k_{nl} * L} \quad (14)$$

Plant maintenance respiration is calculated as a function of the mean leaf nitrogen content. Impacts of the changes to leaf, root, and wood N are described in the supplementary material.

2.4 Model evaluation

The distribution of PFTs was evaluated by first dividing the land surface into eight biomes, based on the 14 World Wildlife Fund terrestrial ecoregions (Olson et al., 2001). The map of biomes (Fig. SM9) acted as a mask for the results to calculate biome-scale averages, and each grid cell was assumed to be 100% composed of the biomes shown in Fig. SM9. For each biome, we calculated the average fractional coverage of each PFT, average gridbox fluxes (GPP and NPP), and average gridbox carbon stocks (soils and vegetation), as well as average fractional coverage of agricultural land. These biome-scaled distributions and averages were then compared to observations. For observed PFT distribution, we used the global vegetation distribution from the European Space Agency’s Land Cover Climate Change Initiative (ESA LCCCI) global vegetation distribution (Poulter et al., 2015; Hartley et al., 2017). To quantify the evaluation of PFT distribution, we calculated an error metric ϵ for each PFT (ϵ_i Eq. 15) and for each biome (ϵ_B Eq. 16). The former enables a ranking of PFTs in terms of their improved distributions and is weighted by biome areas.

The latter enables a comparison between models of the vegetation distribution on a biome scale and implicitly includes an area weighting since all fractions in a biome sum to 1.

$$\varepsilon_{i,PFT} = \sqrt{\frac{\sum_{B=1}^8 A_B (v_{B,i}^{mod} - v_{B,i}^{obs})^2}{\sum_{B=1}^8 A_B}} \quad (15)$$

$$\varepsilon_{B,biome} = \sqrt{\frac{\sum_{i=1}^{npft} (v_{B,i}^{mod} - v_{B,i}^{obs})^2}{npft}} \quad (16)$$

235 ~~where~~ In these equations, A_B is the area of biome B , $npft$ is the number PFTs (in this case 8 because C3 and C4 grasses are combined), and $v_{B,i}$ is the fractional coverage of PFT i in biome B .

To evaluate the carbon fluxes, we used Gross primary productivity (GPP) from the Model Tree Ensemble (MTE; Jung et al., 2011), and MODIS NPP from the MOD17 algorithm (Zhao et al.,
240 2005; Zhao and Running, 2010). Soil and vegetation carbon were from Carvalhais et al. (2014). In addition, we compared biomass stocks to the data set from Ruesch and Gibbs (2008). In all evaluations, we used model years corresponding to the available observation years: 1982-2011 for GPP, 2000-2013 for NPP, and we used a 30-year period for soil and vegetation carbon (1980-2009). All datasets were regridded to the model resolution of 1.25° latitude x 1.875° longitude.

245

3. Model spin up and simulations

3.1 Model simulations

There are a total of ~~six 9~~ simulations: ~~4 one~~ using JULES-C1 and ~~5—five~~ using JULES-C2. Both versions of the model were run with transient climate, CO₂ and land use over the historical period.
250 The climate was from ~~version 6 of CRUNCEP-v6~~, which is a merged dataset of CRU and NCEP reanalysis ~~spanning~~ from 1901 to 2015. Climate variables used were downwelling longwave and shortwave radiation, total precipitation, air temperature, specific humidity, zonal and meridional wind speeds, surface pressure, and a constant diffuse fraction of shortwave radiation of 0.4. The fraction of agriculture in each grid cell was included as fraction of crop and pasture from the

harmonized dataset based on HYDE3.2 (Hurtt et al., 2011). CO₂ concentration was from Dlugokencky and Tans (2013). We ran three additional experiments with JULES-C2 to assess the contributions of climate change, land use change (LUC), and CO₂ fertilization to the changes in carbon cycle components over the historical period (Table 5). Experiment S_{CLIM} was forced with the transient climate from CRUNCEP-v6 to assess the contribution of climate change alone, while atmospheric CO₂ and land use were held to pre-industrial (1860) values. In experiment S_{LUC,CLIM}, climate and land-use changed, while CO₂ was held constant, and in experiment S_{CO2,CLIM}, climate and atmospheric CO₂ changed, while land-use was held constant. For the discussion of attributing changes to these drivers we refer to the main experiment as S_{ALL}, which has transient climate, LUC, and CO₂. The impact of LUC on the present-day carbon cycle is given by S_{ALL}-S_{CO2,CLIM}, and impact of CO₂ fertilization is given by S_{ALL}-S_{LUC,CLIM}. A fifth simulation with JULES-C2 was done to test the model with raw climate model output without bias correction to assess sensitivity of PFT distribution to the climate. This simulation was forced with the HadGEM2-ES RCP2.6 climate and CO₂. The available climate variables from HadGEM2-ES were downwelling longwave and shortwave radiation, stratiform rain, convective rain, stratiform snow, convective snow, air temperature, specific humidity, wind speed, surface air pressure, and the incoming diffuse shortwave radiation.

3.2 Estimating disturbance rates

The simulated distribution of PFTs in TRIFFID is sensitive to the large-scale disturbance parameter γ_v from Eq. (1). The parameter represents several missing processes in JULES related to disturbance-induced mortality (such as fires, pests, and wind events), and provides an estimate of turnover rates for the PFTs. ~~which represents vegetation turnover/mortality from natural processes, and so~~ We developed a method for quickly estimating a global value of γ_v for each PFT. Updated values of γ_v were ~~The estimation was necessary~~ due to new physiology, which resulted in a new NPP per PFT (II in Eq. 1), and an expanded set of PFTs. The method is ~~possible-based on a formula~~

for using the equilibrium distribution of PFTs, made possible by mode of TRIFFID and because of the removal of the hard-wired dominance hierarchy in TRIFFID. Now the equilibrium vegetation fractions are calculated by rearranging Eq. (1), meaning that given by:

$$\lambda_i \Pi_i (1 - \sum_j c_{ij} v_j) = \gamma_{vi} C_{vi} \quad (16)$$

285 And for PFT i , the disturbance rate can be calculated as:

$$\gamma_{vi} = \lambda_i \Pi_i \left[1 - \sum_{j=1}^{npft} c_{ij} v_j \right] * \frac{1}{C_{vi}} \quad (17)$$

where n_{pft} is the number of PFTs.

To estimate new values for γ_{vi} , we ran JULES ~~was run in equilibrium mode~~ for 60 years under present-day climate, CO₂, and land-use, solving for the equilibrium vegetation fractions (as summarized in ~~with a 5 year time step for TRIFFID~~ (see Section 7 of Clark et al., 2011). We used the simulated vegetation carbon (C_v), canopy height (to calculate the competition coefficients c_{ij}), and NPP for spreading ($\lambda \Pi$) at the end of the 60 years, together with the ESA LCCCI observed fraction of PFTs (v_i) (Poulter et al., 2015), to solve for γ_{vi} in each grid cell. The result was a map of

295 ~~In other words, we calculated~~ the γ_v (~disturbance rate) per PFT required to get the observed PFT distribution based on simulated carbon available. Based on global distributions of γ_v for each PFT in grid cells with <50% agriculture from 1950-2012, we used the median value in our simulations (Table 2). The new values of γ_v do not guarantee a perfect simulation of PFT distribution, due to the use of one value per PFT, and because the calculation was based on solving the equilibrium solution

300 to Eq. (1). However, this method does result in a range of γ_v that make physical sense: there are low turnover rates for trees, high turnover rates for grasses, and moderate turnover rates for shrubs.

3.3 Spinning up vegetation and soil carbon

The turnover rates for the four soil carbon pools are 10 yr⁻¹ for DPM, 0.3 yr⁻¹ for RPM, 0.66 yr⁻¹ for microbial biomass, and 0.02 yr⁻¹ for humus (Coleman and Jenkinson, 2014). These are based on experiments on the decomposition of ¹⁴C labelled ryegrass over a 10 year period under field

305

conditions ($\sim 9.3^{\circ}\text{C}$ and > 20 mm of water) (Jenkinson, 1990). The vegetation fractions and soil carbon both require a long initial simulation to reach equilibrium. In a standard simulation, soil carbon spin-up needs to continue for 1,000-2,000 years after vegetation types have stabilized. There are two ways to speed this up: First by solving for vegetation fractions based on the equilibrium solution to Eq. (1) using TRIFFID in an equilibrium mode, which rapidly calculates vegetation fractions for trees and shrubs; and second by using the ‘modified accelerated decomposition’ technique (modified-AD) (Koven et al., 2013). This results in a three-step spin up, summarized below. Note that the first two steps used CRUNCEP-v4, which was available at the beginning of the project.

- 1) Solve for steady-state vegetation fractions in TRIFFID, increasing the time step for TRIFFID and phenology to in equilibrium mode with a time step of 5 years for TRIFFID and 10 days, respectively for phenology. Recycle the climate from the first 20 years of the simulation for a total of 60 years; in this case, CRUNCEP-v6 begins in 1900, so we recycled the 1901-1920 climate. In the simulations with HadGEM2-ES climate, the first 20 years of climate driving data is from 1860-1879. Specify land-use and CO_2 at their 1860 values.
- 2) Modified-AD: Run TRIFFID in dynamic mode with a time step of 1 day for TRIFFID and phenology using accelerated soil turnover rates (Table 3). Recycle climate from the first 20 years of the simulation for a total of 100 years. Initialize soil carbon is initialized to a global constant value of 3 kgC m^{-2} to avoid any unrealistic values of soil carbon calculated during step 1. Specify land-use and CO_2 at their 1860 values.
- 3) Default decomposition: As above but use the default soil carbon turnover times. for 200 years. We initially used 200 years for this phase, but later in the project version 6 of the CRUNCEP climate data became available, so the model was spun up an additional 200 years with the CRUNCEP-v6 data.
- 4) Begin the transient simulation from 1860, using transient CO_2 , land-use, and climate. For CRUNCEP-v6, recycle the 1901-1920 climate for the first 41 years of the simulation.

In the last 100 years of the spin up, soil carbon changed by -0.06% and 0.43% 0.86% with the
335 CRUNCEP-v6 and HadGEM2-ES and CRUNCEP climates, respectively. These drifts are <6
PgC/100 years, or 2.8 ppm/100 years, which is below the C4MIP spin-up requirement for drifts of
less than 10 ppm per century (Fig. SM7 2). Therefore, 300 years is adequate for spinning up the
model, but there is a benefit to using 500 years: the drift in soil carbon in the CRUNCEP-v6 climate
from years 200-299 was -3.5 PgC, compared to only -0.9 PgC from years 400-499.

4. Results

We analyse the results of JULES-C2 with the CRUNCEP-v6 climate against observations, and
against two other models: JULES-C1 with CRUNCEP-v6 and JULES-C2 with HadGEM2-ES.
Globally, the HadGEM2-ES climate has higher precipitation and incoming shortwave radiation at
345 the surface, but lower specific humidity than the CRUNCEP-v6 climate. The average air
temperature is similar until the 1960s, after which CRUNCEP-v6 is slightly warmer (Fig. SM8).

4.1 Predicted vegetation distribution

We evaluate the distribution of vegetation with two methods. First, to compare JULES-C1 and
350 JULES-C2, we aggregate the 9 PFTs into the original 5. Figure 1 shows fractional coverage in
each grid cell of the five vegetation types and bare soil for the models and the observations- (Fig. 1:
BT=broadleaf trees, NT=needle-leaf trees, C3=C3 grasses, C4=C4 grasses, SH=shrubs). Second,
we calculated fractional coverage of each PFT in eight biomes based on the WWF ecoregions (Fig.
2). The eight biomes are tropical forests (TF), extra-tropical mixed forests (MF), boreal forests
355 (BF), tropical savannas (TS), temperate grasslands (TG), tundra (TU), Mediterranean woodland
(Med), and deserts(D) (Figure SM9).

Most carbon in a tree/shrub is stored as woody biomass. Therefore, in terms of vegetation carbon content, the most important distinction between plant types is between trees, grasses, and shrubs.

360 With the CRUNCEP-v6 climate, JULES-C2 represents the distribution of these broad vegetation types very well (Fig. 1). There are several improvements compared to JULES-C1: for example, both the amount of tropical broadleaf trees in the central tropical forests and the spatial extent of boreal forests are more realistic in JULES-C2. The boreal forests in JULES-C1 do not extend far enough across the North American and Eurasian continents. Instead, large areas of shrubs dominate
365 at high latitudes. This bias is reduced in JULES-C2, although there is an underestimation (overestimation) in the coverage of needle-leaf trees in northeastern Eurasia (northern Europe).

Biome-scale distributions of the PFTs are shown in Figure 2, with results from JULES-C2 with both the CRUNCEP-v6 and HadGEM2-ES climates. Differences between JULES-C2 run with
370 ~~CRUNCEP-v6 and HadGEM2-ES~~ different climates are typically small, with a tendency for the climate with higher precipitation to result in more trees (Fig. 3) ($r^2 = 0.66$). Comparing the ESA vegetation fractions and CRUNCEP-v6 climate reveals a weaker positive relationship between tree coverage and annual rainfall ($r^2=0.36$). JULES is also sensitive to the specific humidity ($r^2=0.25$) but this is not supported by the ESA fractions. Coverage of ~~The~~ needle-leaf deciduous trees (~~NDT~~)
375 ~~shows high climate sensitivity, with a large range predicted in the boreal forest;~~ ranges from 16% with the CRUNCEP-v6 climate to 27% with the HadGEM2-ES climate. This PFT was developed to have a competitive advantage in cold, dry environments. ~~The annual average air temperature in the boreal forests is below freezing but precipitation is about 50% higher in the HadGEM2-ES climate compared to the CRUNCEP-v6 climate (Fig. SM8). The HadGEM2-ES climate is relatively colder and drier than CRUNCEP in the larch-dominated regions of Asia, which explains the higher fractions of needle-leaf deciduous trees with this climate.~~
380

Agriculture is shown as a separate category since JULES can only grow ~~either C3 and or C4~~ grasses in the agricultural fraction of grid cells. Agriculture accounts for 22-40% of all biomes except the two high latitude biomes (boreal forests and tundra). To compare with the ESA PFT distributions, we reduce the “observed” agricultural fraction (from the HYDE3.2 dataset) on grid cells where the prescribed agricultural fraction is greater than the coverage of ESA-observed grasses. This discrepancy between the observational datasets results in an apparent overestimation of agricultural fractions in some biomes. Although the agricultural fraction is prescribed, there can be bare soil on agricultural land if the JULES NPP is not sufficient to support vegetation (possibly due to the lack of irrigation in JULES). For this reason, in some biomes the agricultural fraction is underestimated (e.g. in temperate grasslands and deserts with JULES-C1). ~~The fraction of agriculture calculated per biome can vary between the observations and JULES since the data sets for land cover (ESA LCCCI) and for agriculture were produced separately. The model can sometimes underestimate the amount of agricultural land (e.g. in temperate grasslands with JULES C1) if grasses are not productive enough to survive on land where agriculture is prescribed (possibly due to no irrigation applied in JULES).~~

JULES-C2 tends to overestimate the observed coverage of trees by 10-12% in tropical forests and savannahs, and by 3-5% in Mediterranean woodlands. The overestimation of trees in the tropical biomes is due to too much tropical broadleaf evergreen trees (BET-Tr). For example, in the tropical forest biome, 31% of the biome is covered with BET-Tr in the observations compared to a simulated range of 40-44% (with the HadGEM2-ES and CRUNCEP-v6 climates, respectively). The simulated coverage of broadleaf deciduous (~~BDT~~) trees is very realistic in the tropical savannahs. The coverage of dominant tree types is also close to observed in the boreal and mixed forests, with needle-leaf deciduous and evergreen trees in former and broadleaf deciduous and needle-leaf evergreen trees in the latter. However, the coverage of broadleaf deciduous trees is underestimated by 2-6% in both biomes.

410 Grasses are overestimated compared to observations by up to 21% in the boreal forests and tundra. The fractional coverage of bare soil is generally close to observed, with errors <5% for every biome except for tundra, where it is underestimated. In this biome, JULES-C2 produces 10-13% more shrubs and 10-21% more grass than observed. In the temperate grasslands, JULES-C2 with HadGEM2-ES climate overestimates the grass and needle-leaf evergreen tree coverage and
415 underestimates bare soil coverage. Precipitation is almost twice as high in this biome in HadGEM2-ES compared to CRUNCEP-v6 (Fig. SM8). Shrubs in JULES-C2 tend to do best in cold environments: they are underestimated in tropical and mid-latitude biomes, very well simulated in the boreal forests, but overestimated in the tundra biome.

420 The total model biases based on bias per PFT are between 0.55-0.57 for all versions of the model (Table 4). The bias is an area-weighted fractional error per grid cell where the PFT exists (Eq. 15). The PFT biases are reduced for shrubs and grasses, but are higher for broadleaf trees due to too many broadleaf trees in the tropics. The bias for needle-leaf trees in JULES-C2 depends on the climate: the bias is higher with the HadGEM2-ES climate compared to the CRUNCEP-v6 climate.
425 Figure 2 also shows the bias calculated per biome for each simulation (Eq. 16). The biome biases are lowest in JULES-C2 with the HadGEM2-ES climate for five of the biomes, the exceptions being temperate grasslands, tundra, and deserts. In these biomes, the bias is lowest in JULES-C2 with the CRUNCEP-v6 climate. Comparing biomes, JULES-C2 represents vegetation distribution better in boreal and tropical forests than in mixed forests. The tropical savannahs have the highest
430 bias.

4.2 Terrestrial carbon cycle

The patterns of gross and net primary production (GPP and NPP, respectively) simulated by JULES are similar to estimates derived from observations, although JULES fluxes are slightly high (Fig. 4).

435 From 1982-2011, GPP ~~is was~~ 133 PgC yr⁻¹ and 138 PgC yr⁻¹ according to JULES forced with
CRUNCEP-v6 and HadGEM2-ES climate, respectively, compared to observation-based estimates
from the same time period of 123±8 PgC yr⁻¹ (1982-2011; Beer et al., 2010). JULES-C1 with the
CRUNCEP-v6 climate produces ~~a~~ a higher GPP (143 PgC yr⁻¹). GPP is lower in JULES-C2
compared to JULES-C1, and closer to observations, in the tropical biomes (savannahs and forests,
440 Fig. 5a).

From 2000-2013, MODIS estimates ~~a~~ an NPP of ~55 PgC yr⁻¹, compared to 71 and 75 PgC yr⁻¹ in
JULES with the CRUNCEP-v6 and HadGEM2-ES climates, respectively. During the same time
period, JULES-C1 NPP ~~is was~~ 66 PgC yr⁻¹. On average, NPP is 54% of GPP in JULES-C2, while it
445 is 46% in JULES-C1. Both of these are similar to observation-based estimates that NPP should be
roughly half of GPP. In JULES-C2, the largest overestimations of NPP occur in the tropical forests,
savannahs, and mixed forests (Fig. 5b). JULES-C1 has high biases for GPP and NPP in tropical
savannahs due to over-productive C4 grasses, and this bias is reduced in JULES-C2.

450 Global total vegetation carbon is 542 PgC and 553 PgC in JULES-C2 with the CRUNCEP-v6 and
~~climate with the~~ HadGEM2-ES climates, respectively, which is within the range supported by
observations (400-600 PgC, Prentice et al., 2001), and is 65 PgC higher than the dataset from
Ruesch and Gibbs (2008). The high bias mostly occurs in boreal and temperate forests and in
tropical savannahs, where JULES produces more trees than observed (Fig. 5c). The spatial
455 distribution of vegetation carbon is similar to observations (Fig. 4), but due to the extent of the
broadleaf forests the total vegetation carbon in the tropical forest biome is higher than observed.
However, there is large uncertainty in global biomass datasets, for example the tropical savannah
biome in JULES is very comparable to the data from Carvalhais et al. (2014). JULES-C1 has lower
vegetation carbon (468 PgC), with the largest differences between the models being in the tropical
460 forest and savannah biomes. There are two reasons for the increase in C_{veg} for JULES-C2. First,

tropical evergreen and deciduous broadleaf trees are more prevalent in JULES-C2 (Fig. 1). Second, the low vegetation carbon was [previously](#) identified as a bias and the allometric parameters a_{wl} and a_{ws} were increased [for broadleaf trees](#) (Section 2.3.1).

465 The largest biases in JULES occur for soil carbon, which is underestimated in both the high latitudes and the tropics. Globally there is 1422 PgC in JULES-C2 with the CRUNCEP-v6 climate and 1440 PgC with the HadGEM2-ES climate, compared to 2420 PgC in observations and 1362 PgC in JULES-C1. Soil carbon is the result of centuries (or longer) of litter accumulation. Woody PFTs contribute more resistant material to the soil, while grasses turn over carbon in a more
470 decomposable form. Therefore, relatively small differences between simulations in PFT distribution and NPP can contribute to large differences in the soil carbon. For example, in the tropics, soil carbon is higher in JULES-C2 corresponding to the presence of more broadleaf trees and fewer shrubs than in JULES-C1. In addition, due to the increased productivity simulated by JULES-C2, the amount of carbon going into the soils through litterfall is also increased.

475 **4.3 Transient carbon cycle**

Over the past century and according to JULES-C2, the land surface was a net sink of carbon due to an increase in soil carbon (+57 PgC) that offset a smaller decrease in vegetation carbon (-48 PgC) (Fig. 6). The changes in brackets are the average during 2000-2009 minus average during 1900-
480 1909. These changes can be attributed to climate change acting on its own, climate change plus CO₂ fertilization, or climate change plus LUC. In the experiment with climate change only (S_{CLIM} , Table 5), vegetation carbon increases [by](#) 40 PgC, and there [is was](#) a smaller increase in soil carbon since warming encourages decomposition.

485 The effects of CO₂ fertilization and LUC on land carbon are given by the differences between experiments S_{ALL} and $S_{LUC,CLIM}$, and between S_{ALL} and $S_{CO2,CLIM}$, respectively. [Higher levels of](#)

Increased CO₂ over the 20th century results-ed in an additional 63 PgC of soil carbon and 49 PgC of vegetation carbon. This ~~was~~ is due to larger increases in NPP and litterfall than heterotrophic soil respiration (R_h). Both NPP and R_h ~~wer~~-are 58 PgC yr⁻¹ in 1900 in S_{ALL}. NPP increases ~~d~~ to ~72 PgC yr⁻¹, while R_h increases ~~d~~ to 70 PgC yr⁻¹ by the end of the simulation. Land-use change results-ed in a loss of 14 PgC of soil carbon and 124 PgC of vegetation carbon. The largest reductions in vegetation carbon occurred in the tropics and in the eastern U.S. and Europe (Fig. 6). The total land-use source simulated by JULES (138 PgC from 1900-2009) is very close to a recent estimate of total land-use and land cover change emissions of 155±50 PgC from 1901-2012 (Li et al., 2017).

The annual sink is the net biosphere productivity (NBP), or $NPP - R_h$, ~~where R_h is the heterotrophic respiration~~. The simulated NBP from 2000-2009 in JULES-C2 is ~~was~~ 2.1-0±1.0 PgC yr⁻¹. The net land sink simulated by JULES is within the range of estimates from both the Global Carbon Project (1.7±0.8 PgC yr⁻¹ over the same period, Le Quéré et al., 2017) and the IPCC Fifth Assessment Report (AR5) (1.5±0.7 PgC yr⁻¹) (Table 6). The JULES land sink is slightly high compared to the other two estimates, but this ~~is was~~ not the case during the 1980s and 1990s. Excluding LUC, JULES-C2 simulates ~~d~~ an NBP of 3.43 PgC yr⁻¹ in the 2000s, which ~~is was~~ nearly double the natural NBP in the 1980s. The increase ~~is was~~ due to a larger increase in simulated NPP ~~strong uptake-simulated~~ in the experiment without land-use change relative to the increase in R_h (Fig. 6), ~~and in agreement with the high bias in simulated NPP~~. In S_{ALL}, the simulated NBP fluctuates ~~ed~~ around zero until the 1970s, ~~when it began to~~ after which it steadily increases due to the fertilizing effect of atmospheric CO₂. Between 1980-2009, the NBP increases ~~d~~ by 0.08 PgC yr⁻¹ yr⁻¹, ~~which was~~ due to a stronger positive trend in NPP (+0.27 PgC yr⁻¹ yr⁻¹) than in R_h (+0.19 PgC yr⁻¹ yr⁻¹). This increase is not seen in the experiment with preindustrial CO₂.

5. Discussion and Conclusion

Overall JULES with the new nine PFTs produces reasonable present-day distributions of vegetation, GPP, NPP, and vegetation carbon. The largest bias occurs for soil carbon, which is underestimated in regions where observations support—show a high soil carbon content – for example in peatlands and tundra. Global simulated GPP with JULES-C2 with observed climate is (133 PgC yr⁻¹), compared to is slightly higher than GPP derived from up-scaled flux towers (123±8 PgC yr⁻¹; (Beer et al., 2010) and is lower than GPP estimated from oxygen isotopes of atmospheric CO₂ (150-175 PgC yr⁻¹; Welp et al., 2011).

Global NPP according to MODIS is 55 PgC, consistent with another study that evaluated present-day NPP from 251 estimates in the literature and found a mean (±1 standard deviation) of 56.2 (±14.3) PgC yr⁻¹ (Ito, 2011). In comparison, so the JULES NPP (71 PgC yr⁻¹) is slightly too high, which could be reduced by incorporating recent improvements to the parameterization of leaf dark respiration (Huntingford et al., 2017). JULES overestimates NPP in most biomes compared to MODIS, with the exception of deserts and temperate grasslands (Fig. 4). The highest overestimation of NPP is in the tropical forest biome, where JULES predicts a total NPP of 21.0 PgC yr⁻¹ compared to 15.4 PgC yr⁻¹ from MODIS. The MODIS algorithm estimates NPP using parameters derived from a DGVM (BIOME-BGC), climate, and satellite retrievals of land cover, fraction of absorbed photosynthetically available radiation (FPAR), and incoming radiation. Retrievals of reflectances like FPAR can saturate in regions with high vegetation density (Myneni et al., 2002; Lee et al., 2013), meaning that the tropical NPP from MODIS potentially has a low bias in tropical forests. Cloud contamination further complicates satellite retrievals of vegetation properties in the tropics (Cleveland et al., 2015). Future development and evaluation of carbon cycle models would greatly benefit from updated datasets of NPP that incorporate ground-based measurements from long-term networks and that provide uncertainty ranges. Regional products exist, for example the Global Ecosystems Monitoring (GEM) network

(<http://gem.tropicalforests.ox.ac.uk/>) and European National Forest Inventory (Neumann et al., 2016), which could be combined into a global dataset.

540 In a similar version of JULES with prescribed vegetation, simulated GPP and NPP were 128 and 62 PgC yr⁻¹, respectively (during the same time periods presented here) (Harper et al., 2016), compared to 133 and 71 PgC yr⁻¹, respectively, in this study. In that study, differences in PFT-level NPP did not affect the overall vegetation distribution owing to the prescribed distributions used. The simulations presented in the current study use dynamic vegetation, allowing JULES to predict
545 global vegetation distribution. Therefore, the productivity is slightly higher when JULES is allowed to predict vegetation distribution, although the previous study used older versions of CRUNCEP (v4) and JULES (v4.2 – see code availability).

JULES-C2 predicts global biomass of 542-554 PgC, with the largest high biases occurring in the
550 tropics and boreal forests. Early global estimates ranged from 400-600 PgC (Prentice et al. 2001), and the two datasets we analyzed estimate global biomass of 446-487 PgC. A more recent pan-tropical dataset of aboveground biomass suggests even lower vegetation carbon in the tropics (Avitabile et al., 2015). Despite the uncertainty in global biomass and NPP datasets, the fact that JULES overestimates both NPP and C_{veg} in most biomes supports the conclusion that JULES net
555 productivity is too high. It's also possible that the allometric parameters a_{wl} and a_{ws} should be reduced following further evaluation of biomass predicted with the new PFTs. ~~The tendency for JULES tends to overestimate the tree coverage and underestimate coverage by shrubs, also which also contributes to result in high biomass. —i.e. very productive—Woody trees dominate are dominating in regions where in reality shrubs form a larger proportion of the landscape, such as~~
560 tropical savannahs and Mediterranean woodlands (Fig. 1, 2). In subtropical forests, the model simulates too many broadleaf trees and virtually no shrubs. ~~In addition, JULES lacks an interactive~~

fire model, which would In both regions (outside of the central tropical forests), fires reduce woody vegetation cover but this process is missing in the model.

565 NPP is an essential component of the JULES simulation since it largely determines the competitive advantage of a PFT. Unfortunately, the only available global dataset of NPP is a satellite derived product (MOD17), which does not directly measure NPP, but instead uses a model to estimate NPP using a DGVM (BIOME-BGC) constrained by land cover, fraction of absorbed photosynthetically available radiation observed from space, incoming radiation and climate. Therefore, a direct match
570 between JULES and the MODIS NPP is not the aim of model development, but it is still useful to compare the large-scale fluxes.

Based on these evaluations, we highlight four priorities for developments of JULES vegetation: interactive fires, vegetation in semi-arid environments, impacts of soil moisture stress on vegetation, and tundra/high latitude vegetation. Interactive fires are an important missing process.

575 The simulation without land-use change (experiment S_{CLIM,CO2 +}) shows a large overestimation of biomass in the cerrado region of Brazil, where fires (in addition to human land clearing) likely limit vegetation coverage. Interactive fires could also help with the overestimation of trees and underestimation of shrubs, since shrubs occur earlier in the successional stages following a fire than trees. A lack of shrubs in tropical savannahs and Mediterranean woodlands These are also biomes
580 in dry or semi-arid climates also implies that Based on this we suggest focusing future development of PFTs should focus on vegetation characteristic of these biomes – for example drought-tolerant shrubs with phenology that responds to moisture as well as temperature. Such development should also take into account uncertainties in observed vegetation distributions in these regions (Hartley et al. 2017). The lack of vegetation in arid environments could also be due to plants experiencing too
585 much moisture-related stress as soils dry, or to soils drying too rapidly following a rain event. A revised parameterisation of soil moisture stress or more sophisticated vegetation hydraulics scheme would likely improve the model in these regions. Previous work also pointed to soil moisture stress

as a likely culprit for underestimated dry season GPP at two towers in the Brazilian Amazon and for too low GPP at a non-irrigated maize site (Harper et al., 2016; Williams et al., 2017). Another large bias is the prevalence of shrubs in the tundra biome and therefore more tundra-specific PFTs could improve the simulation in these regions. The importance of such developments should not be understated – climate change will likely bring a widening of subtropical dry zones and warmer temperatures at high latitudes, so these regions will be areas of large changes in vegetation in the future and will play key roles the evolving carbon cycle and ecosystem distribution of the 21st century.

JULES vegetation distribution and productivity fluxes seem robust to small differences in the climate based on the simulation with HadGEM2-ES climate, implying that different climate driving datasets should not result in large differences in vegetation distribution. Global mean GPP, NPP, and C_{veg} simulated with the two different climates varies by 5%, 7%, and <1%, respectively. Vegetation distributions are broadly the same as well, ~~although the extent of simulated trees is sensitive to precipitation with an exception being the distribution of needle leaf deciduous trees which seem relatively more sensitive to air temperature precipitation and humidity~~. In contrast, simulated values of C_{soil} have significant variation depending on the climate data used, since the soil carbon accumulates over centuries and is therefore sensitive to small differences in vegetation distribution and productivity. Global C_{soil} is similar between the two simulations with JULES-C2, but the distribution has large regional differences (not shown). In the case of soil carbon, the mismatch between simulated and observed is greater than the range between simulations.

Compared to the best available estimates of the annual terrestrial carbon sink, the JULES simulation is well within the range (2.0 ± 1.0 PgC yr⁻¹ from 2000-2009). However, without nutrient limitation in this version of the model, it's possible that the positive trend in NBP is too high in JULES, as indicated by the large simulated increase in NBP between the 1990s and 2000s in the experiment

without land-use change, which ~~was~~ is not found in the IPCC AR5 or GCP results. Although
615 simulated NBP in the 1980s is bounded by the estimates from GCP and IPCC, the simulated NBP
in the 2000s is higher than both constraints, indicating that either the increase in NPP is too large, or
the response from R_h is too low. Anecdotally, the high bias in NPP (Fig. 4, 5) supports the former,
but this doesn't rule out the possibility that respiration was undersensitive to climate and CO₂ over
this period and the transient responses over the past 30 years should be further evaluated.

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Code availability

630 This work was based on a version of JULES4.6 with some additional developments that will be
included in UKESM. The code is available from the JULES FCM repository:
<https://code.metoffice.gov.uk/trac/jules> (registration required). The version used was
r4546_UKESM (located in the repository at branches/dev/annaharper/r4546_UKESM). Two suites
are available to replicate the factorial experiments with CRUNCEP-v6 climate: u-ao199 and u-
635 ao216.

References

- Avitabile, V., Herold, M., Heuvelink, G. B. M., Lewis, S. L., Phillips, O. L., Asner, G. P., Armston, J., Ashton, P. S., Banin, L., Bayol, N., Berry, N. J., Boeckx, P., Jong, B. H. J., DeVries, B.,
640 Girardin, C. A. J., Kearsley, E., Lindsell, J. A., Lopez - Gonzalez, G., Lucas, R., Malhi, Y., Morel, A., Mitchard, E. T. A., Nagy, L., Qie, L., Quinones, M. J., Ryan, C. M., Ferry, S. J. W., Sunderland, T., Laurin, G. V., Gatti, R. C., Valentini, R., Verbeeck, H., Wijaya, A., and Willcock, S.: An integrated pan - tropical biomass map using multiple reference datasets, *Global Change Biology*, 22, 1406-1420, 10.1111/gcb.13139, 2015.
- 645 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K. W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I., and Papale, D.: Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate, *Science*, 329, 834, 10.1126/science.1184984, 2010.
- 650 Best, M. J., Pryor, M., Clark, D. B., Rooney, G. G., Essery, R. L. H., Ménard, C. B., Edwards, J. M., Hendry, M. A., Porson, A., Gedney, N., Mercado, L. M., Sitch, S., Blyth, E., Boucher, O., Cox, P. M., Grimmond, C. S. B., and Harding, R. J.: The Joint UK Land Environment Simulator (JULES), model description – Part 1: Energy and water fluxes, *Geosci. Model Dev.*, 4, 677-699, <https://doi.org/10.5194/gmd-4-677-2011>, 2011.
- 655 Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J. T., and Reichstein, M.: Global covariation of carbon turnover times with climate in terrestrial ecosystems, 514, 213, 10.1038/nature13731, 2014.
- 660 Clark, D., Mercado, L., Sitch, S., Jones, C., Gedney, N., Best, M., Pryor, M., Rooney, G., Essery, R., Blyth, E., Boucher, O., Harding, R., Huntingford, C., and Cox, P.: The Joint UK Land Environment Simulator (JULES), model description - Part 2: Carbon fluxes and vegetation dynamics, *Geoscientific Model Development*, 4, 701-722, 10.5194/gmd-4-701-2011, 2011.
- 665 Cleveland, C. C., Taylor, P., Chadwick, K. D., Dahlin, K., Doughty, C. E., Malhi, Y., Smith, W. K., Sullivan, B. W., Wieder, W. R., and Townsend, A. R.: A comparison of plot - based satellite and Earth system model estimates of tropical forest net primary production, *Global Biogeochemical Cycles*, 29, 626-644, 10.1002/2014GB005022, 2015.
- Coleman, K., and Jenkinson, D. S.: A model for the turnover of carbon in soil, Rothamsted Research Harpenden Herts AL5 2JQ, United Kingdom, 44, 2014.
- 670 Cox, P. M., Huntingford, C., and Harding, R. J.: A canopy conductance and photosynthesis model for use in a GCM land surface scheme, *Journal of Hydrology*, 212-213, 79-94, 10.1016/S0022-1694(98)00203-0, 1998.
- Cox, P. M.: Description of the TRIFFID dynamic global vegetation model, Hadley Centre, Met Office, London Road, Bracknell, Berks, RG122SY, UK, 17, 2001.
- 675 Enquist, B. J., Brown, J. H., and West, G. B.: Allometric scaling of plant energetics and population density, *Nature*, 395, 163-166, 1998.
- Fisher, J. B., Huntzinger, D. N., Schwalm, C. R., and Sitch, S.: Modelling the Terrestrial Biosphere, *Annu. Rev. Environ. Resour.*, 39, 91-123, <https://doi.org/10.1146/annurev-environ-012913-093456>, 2014.

- 680 Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochemical Cycles*, 10, 603-628, 1996.
- Friend, A. D., Shugart, H. H., and Running, S. W.: A physiology-based model of forest dynamics, *Ecology*, 74, 792-797, 1993.
- 685 Harper, A. B., Cox, P. M., Friedlingstein, P., Wiltshire, A. J., Jones, C. D., Sitch, S., Mercado, L. M., Groenendijk, M., Robertson, E., Kattge, J., Bönisch, G., Atkin, O. K., Bahn, M., Cornelissen, J., Niinemets, Ü., Onipchenko, V., Peñuelas, J., Poorter, L., Reich, P. B., Soudzilovskaia, N. A., and Bodegom, P. V.: Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4.2) using plant trait information, *Geosci. Model Dev.*, 9, 2415-2440, doi.org/10.5194/gmd-9-2415-2016, 2016.
- 690 Hartley, A. J., MacBean, N., Georgievski, G., and Bontemps, S.: Uncertainty in plant functional type distributions and its impact on land surface models, *Remote Sensing of Environment*, 203, 71-89, 10.1016/j.rse.2017.07.037, 2017.
- Hillis, W. E.: *Heartwood and Tree Exudates*, Springer Series in Wood Science, Springer-Verlag Berlin Heidelberg, 268 pp., 1987.
- 695 Huntingford, C., Yang, H., Harper, A., Cox, P. M., Gedney, N., Burke, E. J., Lowe, J. A., Hayman, G., Collins, B. J., Smith, S. M., and Comyn-Platt, E.: Flexible parameter-sparse global temperature time-profiles that stabilise at 1.5°C and 2.0°C, *Earth Syst. Dynam. Discuss.*, 2017, 1-11, 10.5194/esd-2017-17, 2017.
- 700 Hurtt, G. C., Chini, L. P., Frolking, S., Betts, R. A., Feddema, J., Fischer, G., Fisk, J. P., Hibbard, K., Houghton, R. A., Janetos, A., Jones, C. D., Kindermann, G., Kinoshita, T., Klein Goldewijk, K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., van Vuuren, D. P., and Wang, Y. P.: Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands, *Climatic Change*, 109, 117, 10.1007/s10584-011-0153-2, 2011.
- 705 Ito, A.: A historical meta-analysis of global terrestrial net primary productivity: are estimates converging?, *Global Change Biology*, 17, 3161-3175, 2011.
- Jenkinson, D. S.: Quantitative theory in soil productivity and environmental pollution - The turnover of organic carbon and nitrogen in soil, *Philos Trans R Soc Lond B Biol Sci*, 329, 361, 10.1098/rstb.1990.0177, 1990.
- 710 Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., Arneth, A., Bernhofer, C., Bonal, D., Chen, J., Gianelle, D., Gobron, N., Kiely, G., Kutsch, W., Lasslop, G., Law, B. E., Lindroth, A., Merbold, L., Montagnani, L., Moors, E. J., Papale, D., Sottocornola, M., Vaccari, F., and Williams, C.: Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations, *Journal of Geophysical Research: Biogeosciences*, 116, n/a-n/a, 2011.
- 715 Koven, C. D., Riley, W. J., Subin, Z. M., Tang, J. Y., Torn, M. S., Collins, W. D., Bonan, G. B., Lawrence, D. M., and Swenson, S. C.: The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4, *Biogeosciences*, 10, 7109-7131, 10.5194/bg-10-7109-2013, 2013.
- 720 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C., Korsbakken, J. I., Peters, G. P., Canadell, J. G., Jackson, R. B., Boden, T. A., Tans, P. P., Andrews,

- O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L., Chevallier, F., Chini, L. P., Ciais, P., Cosca, C. E., Cross, J., Currie, K., Gasser, T., Harris, I., Hauck, J.,
725 Haverd, V., Houghton, R. A., Hunt, C. W., Hurtt, G., Ilyina, T., Jain, A. K., Kato, E., Kautz, M., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P. M. S., Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., Nojiri, Y., Padín, X. A., Peregon, A., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I.,
730 Stocker, B. D., Tian, H., Tilbrook, B., van der Laan-Luijkx, I. T., van der Werf, G. R., van Heuven, S., Viovy, N., Vuichard, N., Walker, A. P., Watson, A. J., Wiltshire, A. J., Zaehle, S., and Zhu, D.: Global Carbon Budget 2017, *Earth Syst. Sci. Data Discuss.*, 2017, 1-79, 10.5194/essd-2017-123, 2017.
- Lee, J.-E., Frankenberg, C., van der Tol, C., Berry, J. A., Guanter, L., Boyce, C. K., Fisher, J. B.,
735 Morrow, E., Worden, J. R., Asefi, S., Badgley, G., and Saatchi, S.: Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll fluorescence, *Proceedings of the Royal Society - Biological Sciences*, 280, 10.1098/rspb.2013.0171, 2013.
- Li, W., Ciais, P., Peng, S., Yue, C., Wang, Y., Thurner, M., Saatchi, S. S., Arneeth, A., Avitabile, V.,
740 Carvalhais, N., Harper, A. B., Kato, E., Koven, C., Liu, Y. Y., Nabel, J. E. M. S., Pan, Y., Pongratz, J., Poulter, B., Pugh, T. A. M., Santoro, M., Sitch, S., Stocker, B. D., Viovy, N., Wiltshire, A., Yousefpour, R., and Zaehle, S.: Land-use and land-cover change carbon emissions between 1901 and 2012 constrained by biomass observations, *Biogeosciences*, 14, 5053-5067, 10.5194/bg-14-5053-2017, 2017.
- Lloyd, J., Patiño, S., Paiva, R. Q., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., Baker, T. R.,
745 Brand, W. A., Hilke, I., Gielmann, H., Raessler, M., Luizão, F. J., Martinelli, L. A., and Mercado, L. M.: Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees, *Biogeosciences*, 7, 1833-1859, 10.5194/bg-7-1833-2010, 2010.
- Mangeon, S., Voulgarakis, A., Gilham, R., Harper, A., Sitch, S., and Folberth, G.: INFERNO: a fire
750 and emissions scheme for the UK Met Office's Unified Model, *Geosci. Model Dev.*, 9, 2685-2700, 10.5194/gmd-9-2685-2016, 2016.
- Myneni, R. B., Hoffman, S., Knyazikhin, Y., Privette, J. L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G. R., Lotsch, A., Friedl, M., Morisette, J. T., Votava, P., Nemani, R. R., and Running, S. W.: Global products of vegetation leaf area and fraction absorbed PAR from year one
755 of MODIS data, *Remote Sensing of Environment*, 83, 214-231, 10.1016/S0034-4257(02)00074-3, 2002.
- Neumann, M., Moreno, A., Thurnher, C., Mues, V., Härkönen, S., Mura, M., Bouriaud, O., Lang, M., Cardellini, G., Thivolle-Cazat, A., Bronisz, K., Merganic, J., Alberdi, I., Astrup, R., Mohren, F., Zhao, M., and Hasenauer, H.: Creating a Regional MODIS Satellite-Driven Net Primary Production
Dataset for European Forests, *Remote Sensing*, 8, 10.3390/rs8070554, 2016.
- 760 Niklas, K. J., and Spatz, H.-C.: Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass, *Proc Natl Acad Sci U S A*, 101, 15661-15663, 10.1073/pnas.0405857101, 2004.
- Ogawa, K.: Mathematical consideration of the pipe model theory in woody plant species, *Trees*, 29, 695-704, 10.1007/s00468-014-1147-2, 2015.
- 765 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts,

- T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R.: Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity, *BioScience*, 51, 933-938, 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2, 2001.
- 770 Poulter, B., MacBean, N., Hartley, A., Khlystova, I., Arino, O., Betts, R., Bontemps, S., Boettcher, M., Brockmann, C., Defourny, P., Hagemann, S., Herold, M., Kirches, G., Lamarche, C., Lederer, D., Ottlé, C., Peters, M., and Peylin, P.: Plant functional type classification for earth system models: results from the European Space Agency's Land Cover Climate Change Initiative, *Geosci. Model Dev.*, 8, 2315-2328, 10.5194/gmd-8-2315-2015, 2015.
- 775 Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., and Solomon, A. M.: Special Paper: A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate, *Journal of Biogeography*, 19, 117-134, 10.2307/2845499, 1992.
- 780 Prentice, I. C., Farquhar, G. D., Fasham, M. J. R., Goulden, M. L., Heimann, M., Jaramillo, V. J., Kheshgi, H. S., Le Quéré, C., Scholes, R. J., and Wallace, D. W. R.: The Carbon Cycle and Atmospheric Carbon Dioxide, in: *Climate Change 2001: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* edited by: Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., and Johnson, C. A., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., 183-237, 2001.
- 785 Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., and Sykes, M. T.: Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change, in: *Terrestrial Ecosystems in a Changing World. Global Change — The IGBP Series.*, edited by: Canadell J.G., P. D. E., Pitelka L.F., Springer, Berlin, Heidelberg, 175-192, 2007.
- 790 Ruesch, A., and Gibbs, H. K.: New IPCC Tier-1 Global Biomass Carbon Map For the Year 2000. Carbon Dioxide Information Analysis Center (Ed.), Oak Ridge National Laboratory, Oak Ridge, Tennessee, 2008.
- 795 Running, S. W., and Gower, S. T.: FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets, *Tree Physiology*, 9, 147-160, 10.1093/treephys/9.1-2.147, 1991.
- 800 Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161-185, 2003.
- 805 Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlström, A., Doney, S. C., Graven, H., Heinze, C., Huntingford, C., Levis, S., Levy, P. E., Lomas, M., Poulter, B., Viovy, N., Zaehle, S., Zeng, N., Arneth, A., Bonan, G., Bopp, L., Canadell, J. G., Chevallier, F., Ciais, P., Ellis, R., Gloor, M., Peylin, P., Piao, S. L., Le Quéré, C., Smith, B., Zhu, Z., and Myneni, R.: Recent trends and drivers of regional sources and sinks of carbon dioxide, *Biogeosciences*, 12, 653-679, 10.5194/bg-12-653-2015, 2015.
- Welp, L. R., Keeling, R. F., Meijer, H. A. J., Bollenbacher, A. F., Piper, S. C., Yoshimura, K., Francey, R. J., Allison, C. E., and Wahlen, M.: Interannual variability in the oxygen isotopes of atmospheric CO₂ driven by El Niño, 477, 579, 10.1038/nature10421, 2011.

810 Williams, K., Gornall, J., Harper, A., Wiltshire, A., Hemming, D., Quaife, T., Arkebauer, T., and
Scoby, D.: Evaluation of JULES-crop performance against site observations of irrigated maize from
Mead, Nebraska, *Geosci. Model Dev.*, 10, 1291-1320, 10.5194/gmd-10-1291-2017, 2017.

Woodward, F. I.: *Climate and Plant Distribution*, Cambridge University Press, 1987.

815 Zhao, M., Heinsch, F. A., Nemani, R. R., and Running, S. W.: Improvements of the MODIS
terrestrial gross and net
primary production global data set, *Remote Sensing of Environment*, 95, 164-176,
10.1016/j.rse.2004.12.011, 2005.

820 Zhao, M., and Running, S. W.: Drought-induced reduction in global terrestrial net
primary production from 2000 through 2009, *Science*, 329, 940, 10.1126/science.1192666, 2010.

5 PFTs (JULES-C1)	9 PFTs (JULES-C2)
Broadleaf trees (BT)	Tropical broadleaf evergreen trees (BET-Tr)
Needle-leaf trees (NT)	Temperate broadleaf evergreen trees (BET-Te)
C3 grass (C3)	Broadleaf deciduous trees (BDT)
C4 grass (C4)	Needle-leaf evergreen trees (NET)
Shrubs (SH)	Needle-leaf deciduous trees (NDT)
	C3 grass (C3)
	C4 grass (C4)
	Evergreen shrubs (ESH)
	Deciduous shrubs (DSH)

Table 1. The original five and new nine PFTs in JULES.

	BET-Tr	BET-Te	BDT	NET	NDT	C3 grass	C4 grass	ESH	DSH
a_{wl}	0.845	0.78	0.78	0.65	0.80	0.005	0.005	0.13	0.13
a_{ws}	13	12	12	10	10	1	1	13	13
n_{sw}	0.0072	0.0072	0.0072	0.0083	0.0083	0.01604	0.0202	0.0072	0.0072
n_r	0.01726	0.01726	0.01726	0.00784	0.00784	0.0162	0.0084	0.01726	0.01726
γ initial	0.005	0.005	0.005	0.007	0.007	0.20	0.20	0.05	0.05
γ from Eq. 17	0.007	0.014	0.007	0.020	0.010	0.25	0.06	0.10	0.06

Table 2. Updated parameters for vegetation carbon, root and stem nitrogen in JULES-C2. The parameters are: a_{wl} relates wood to leaf carbon (kg C m^{-2} per unit LAI), a_{ws} is the ratio of total wood carbon to respiring stem carbon, n_r is the ratio of root N to root C, n_{sw} is the ratio of stemwood N to stem C, γ is the large-scale disturbance parameter ($\text{kg C m}^{-2} 360 \text{ d}^{-1}$).

	RPM	DPM	BIO	HUM
Default (s^{-1})	3.17×10^{-7}	9.6×10^{-9}	2.1×10^{-8}	6.4×10^{-10}
Accelerated (s^{-1})	3.17×10^{-7}	3.17×10^{-7}	3.15×10^{-7}	3.2×10^{-7}
Factor	1	33	15	500

Table 3. Turnover rates for the four soil carbon pools (RPM = resistant plant material; DPM = decomposable plant material; BIO = microbial biomass; HUM = humus). The factor is used to rescale soil carbon pools between the “fast” and “slow” spin ups.

PFT	JULES-C2 CRUNCEP	JULES-C2 HadGEM2	JULESC1- CRUNCEP
Bet-Tr	0.15	0.14	0.13 (for all BT)
BET-Te	0.017	0.015	--
BDT	0.063	0.049	--
NET	0.078	0.12	0.15 (for all NT)
NDT	0.043	0.044	--
Grasses	0.088	0.096	0.11
ESH	0.053	0.054	0.17 (for all Shrubs)
DSH	0.054	0.056	--
Total bias	0.55	0.57	0.56

Table 4. Bias in PFT distribution for JULES-C2 run with two different climates and JULES-C1 run with the CRUNCEP climate.

	JULES-C2 (S_{CLIM})	JULES-C2 (S_{ALL})	JULES-C2 (S_{CLIM,LUC})	JULES-C2 (S_{CLIM,CO2})
Experiment summary	Transient climate change only	Transient CO ₂ , land-use, and climate change	Transient climate and LUC	Transient climate and CO ₂
ΔC_{soil} (PgC)	8	57	-6	71
ΔC_{veg} (PgC)	40	-48	-97	75

Table 5. Simulated change in average fluxes and stocks from the period 1900-1909 to 2000-2009 in JULES-C2. Positive values indicate a gain of carbon by the land surface.

	1980-1989	1990-1999	2000-2009
<i>Net land sink</i>			
JULES-C2 (NBP in S_{ALL})	0.5 4 ±1.1	1.1 0 ±0.8	2.1 0 ±1.0
IPCC AR5	0.1±0.6	1.1±0.7	1.5±0.7
GCP 2017 ($S_{land}-E_{LUC}$)	0.7±0.7	1.2±0.5	1.7±0.8
<i>Emissions from LUC</i> JULES-C2			
(NBP, $S_{CLIM,CO2}-S3_{ALL}$)	-1.2±1.1	-1.3±0.9	-1.3±1.0
IPCC AR5: net LUC ¹	-1.4±0.6	-1.5±0.6	-1.1±0.6
GCP 2017 (E_{LUC}) ²	-1.2±0.7	-1.3±0.7	-1.2±0.7
<i>Residual Land sink</i>			
JULES-C2 (NBP in $S_{CLIM,CO2}$)	1.7 6 ±1.1	2.4 3 ±0.9	3.4 3 ±1.0
IPCC AR5	1.5±0.8	2.6±0.9	2.6±0.9
GCP 2017 (S_{land})	2.0±0.6	2.5±0.5	2.9±0.8

¹ Using the bookkeeping LUC flux accounting model of Houghton et al. (2012).

² Bookkeeping methods

Table 6. Estimates of net land sink, emissions due to land-use change, and the “residual” sink on land from JULES compared to two other methods. Uncertainty ranges were reported differently for each method: for JULES $\pm 1\sigma$ indicates the interannual variability of the annual mean, the IPCC reported a 90% confidence interval (based on GCP 2013) which here is converted to $\pm 1\sigma$, and GCP reported $\pm 1\sigma$ of the decadal mean across DGVMs for S_{land} and $\pm 1\sigma$ of bookkeeping estimates for E_{LUC} .

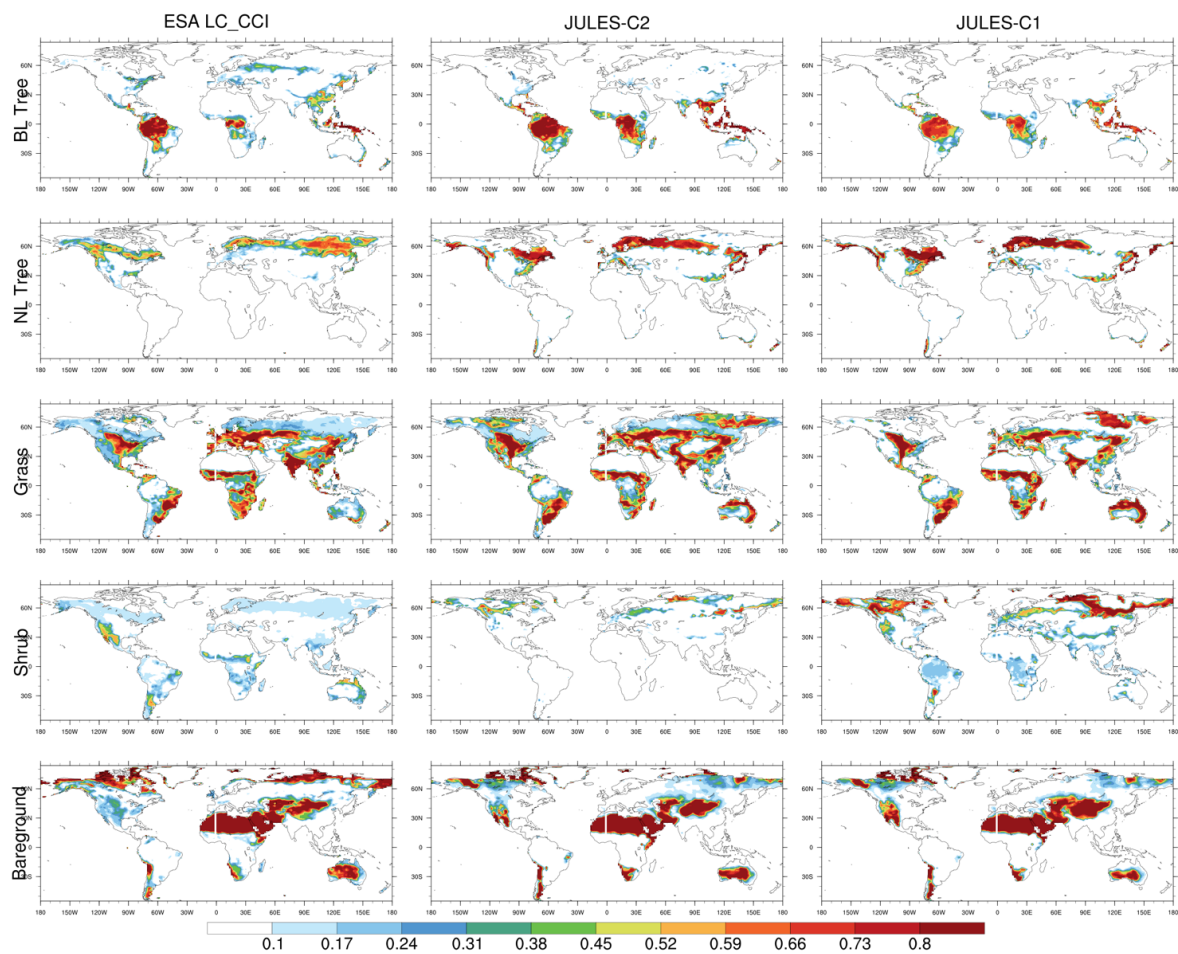


Figure 1: Distribution Fraction of land in each grid cell covered by ~~of~~ vegetation and bare soil over the period 2010-2014 in the ESA LC-CCI dataset (left column), and JULES-C2 with CRUNCEP climate (middle column), and JULES-C1 with CRUNCEP climate (right column). BL = broadleaf; NL = needle-leaf.

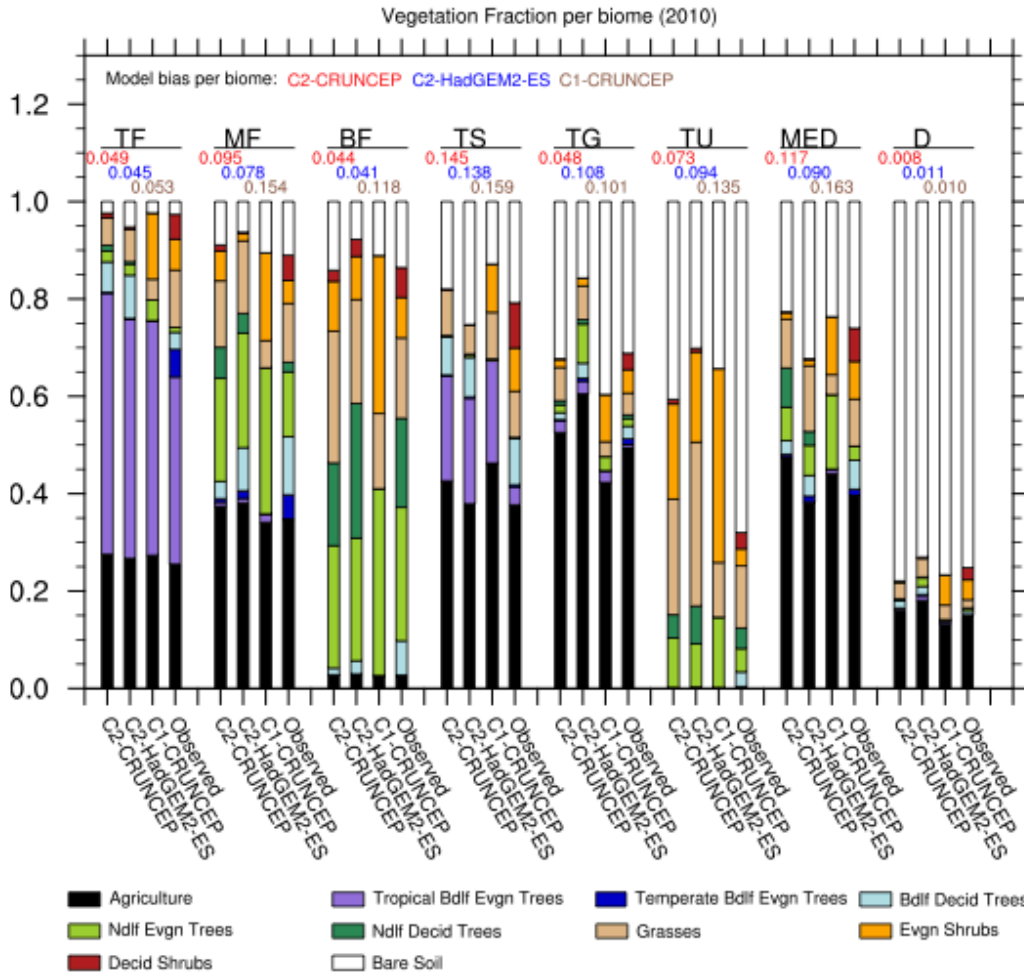


Figure 2: Comparison of PFT distribution by biome in JULES-C2 forced with CRUNCEP^{v6} and HadGEM2-ES climates, compared to JULES-C1 with CRUNCEP^{v6} climate and to the observed distribution from ESA LC-CCI. TF: Tropical Forests; MF: Temperate Mixed Forests; BF: Boreal Forests; TS: Tropical Savannah; TG: Temperate Grasslands; TU: Tundra; MED: Mediterranean Woodlands; D: Deserts (biomes in Fig. SM9). The black bars represent agricultural land. Model biases per biome are from Eq. (16).

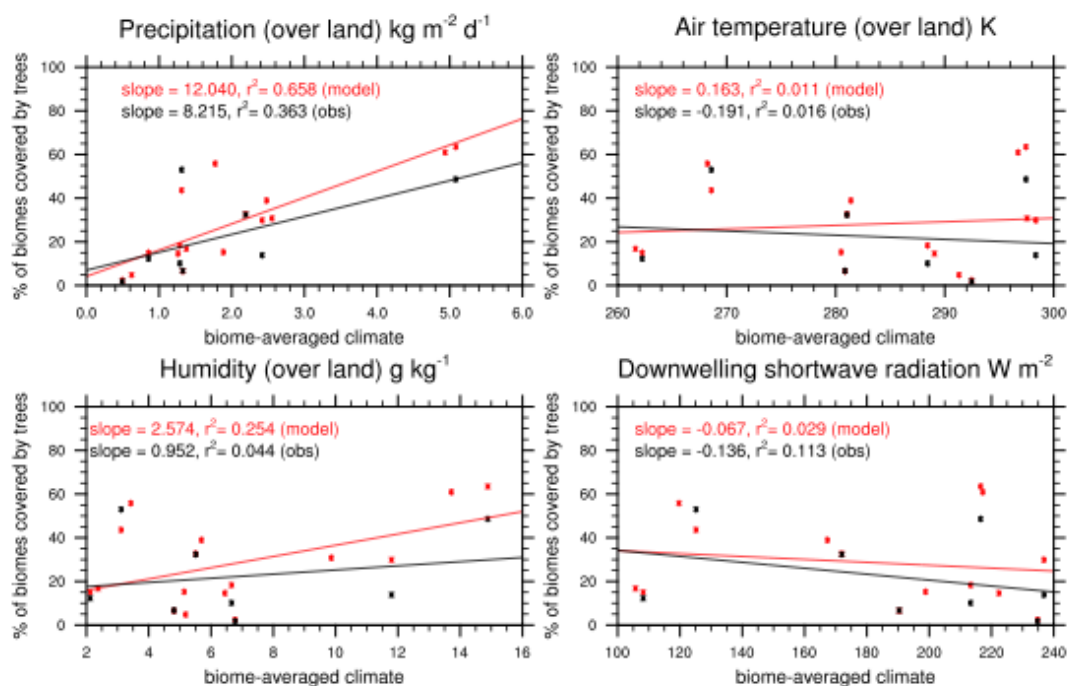


Figure 3: Sensitivity of simulated tree coverage in each biome to precipitation, air temperature, specific humidity, and shortwave radiation. Model results are from JULES with both CRUNCEP-v6 and HadGEM2-ES climates. The observations compare the ESA LC-CCI land cover to the observed (CRUNCEP-v6) climate.

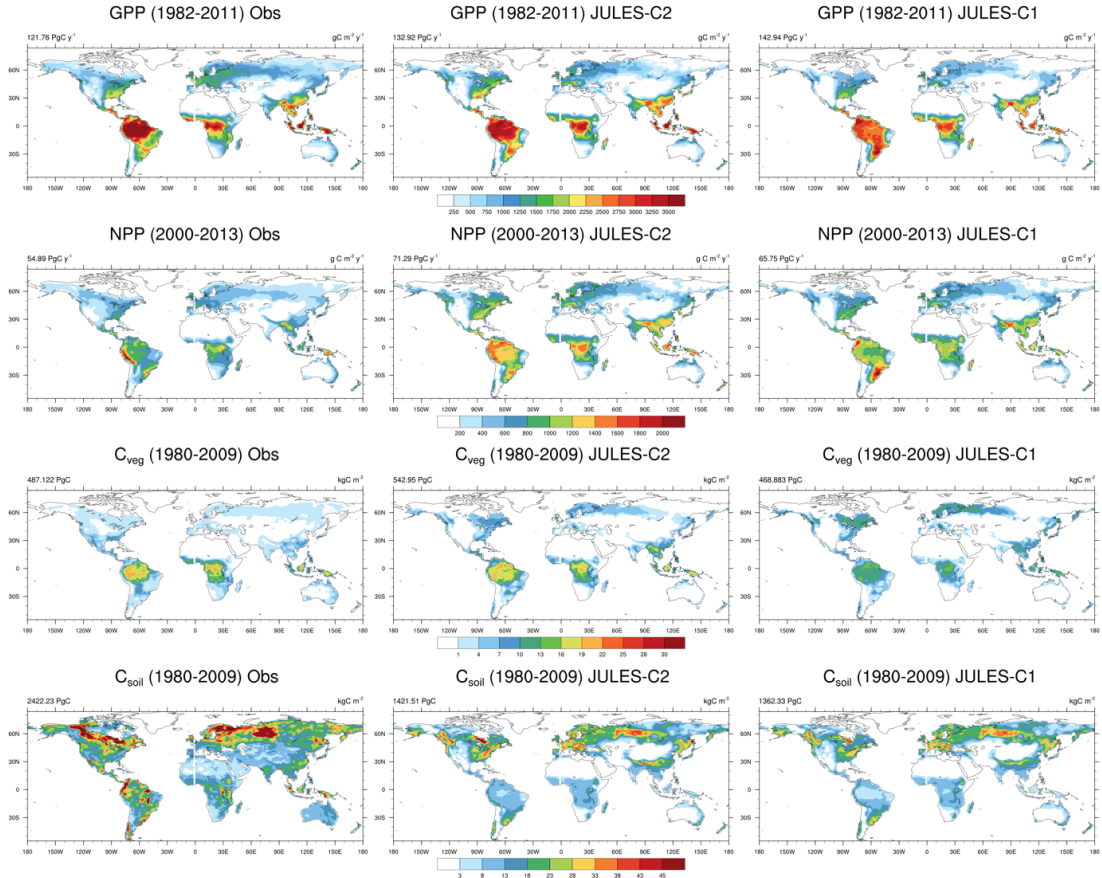


Figure 4: Simulated and observed GPP, NPP, vegetation and soil carbon. Results are shown from JULES-C2 and JULES-C1 both with CRUNCEP climate. Sources for observations are: GPP: FLUXNET-derived model tree ensemble (Jung et al., 2011); NPP: MODIS17 (Zhao et al., 2005b); C_{veg} : Ruesch and Gibbs (2008); C_{soil} : Carvalhais et al. (2014).

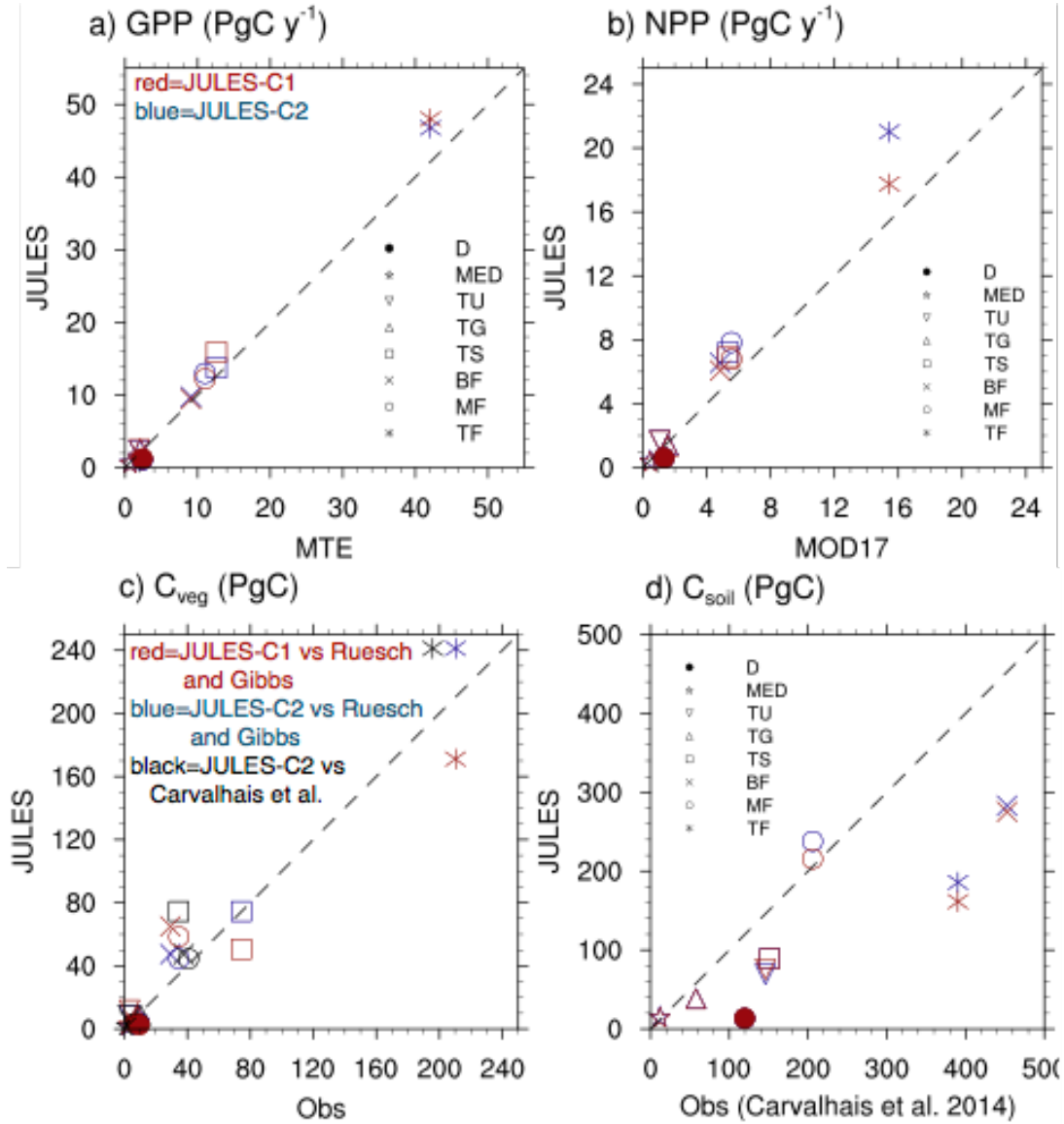


Figure 5: Biome-averaged (a) GPP, (b) NPP, (c) C_{veg}, and (d) C_{soil} in JULES-C1 and JULES-C2 (both with CRUNCEP-v6 climate) compared to observations. The observation sources are the same as in Fig. 3 except (c) includes the C_{veg} from Carvalhais et al. (2014) (black shapes). The biomes are TF: Tropical Forests; MF: Temperate Mixed Forests; BF: Boreal Forests; TS: Tropical Savannah; TG: Temperate Grasslands; TU: Tundra; MED: Mediterranean Woodlands; D: Deserts (biomes in Fig. SM8). Grid cells with >50% agriculture have been excluded from the biome averages.

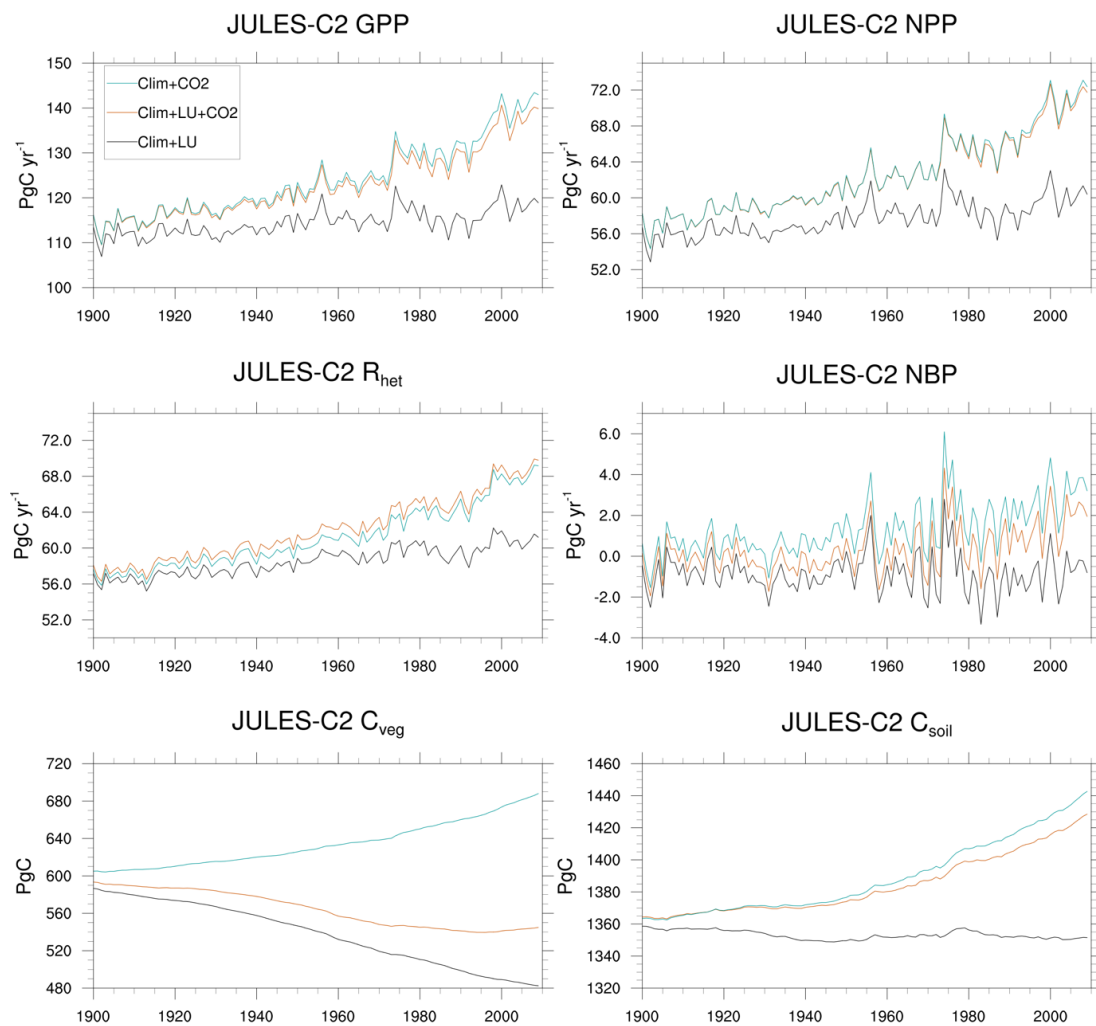


Figure 6: Global mean gross primary productivity (GPP), net primary productivity (NPP), heterotrophic respiration (R_{het}), net biome productivity ($NBP = GPP - R_{het}$), vegetation carbon (C_{veg}), and soil carbon (C_{soil}). Global means are shown for the experiment with transient climate change only (S1), transient climate change and land-use change (S2), and S2 plus transient CO₂ (S3).

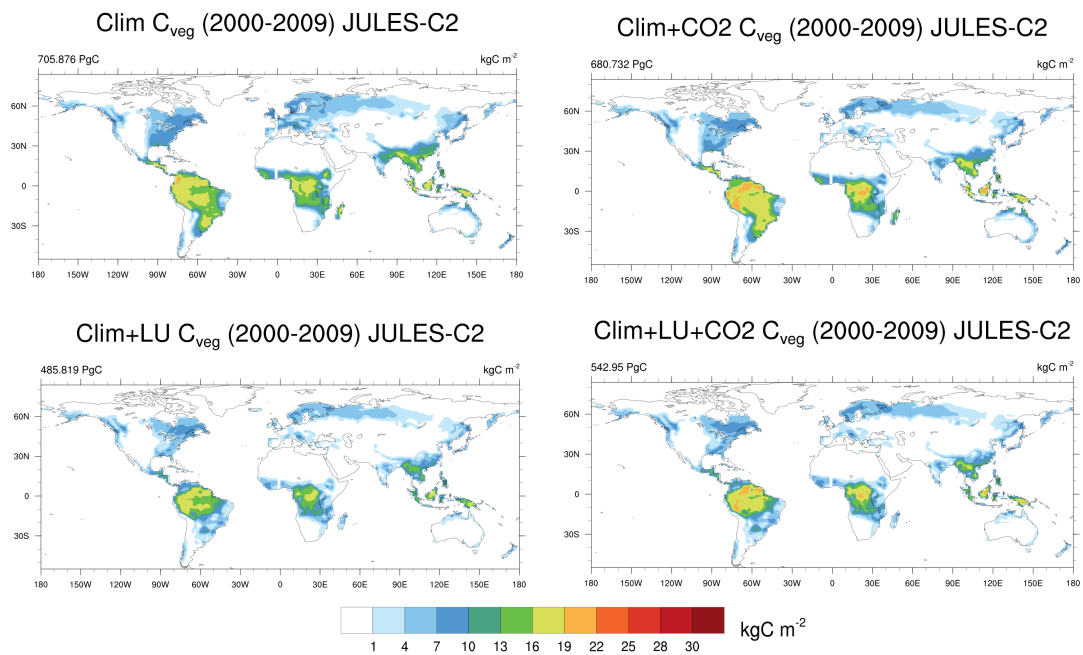


Figure 7: Global distribution of vegetation carbon in JULES-C2 in experiments with and without transient land-use and CO₂.