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LETTER

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Robinson I Negrón-Juárez¹, Charles D Koven, William J Riley, Ryan G Knox and Jeffrey Q Chambers

Lawrence Berkeley National Laboratory, Earth Sciences Division, 1 Cyclotron Rd., MS74R316C, Berkeley, CA 94720, USA

¹ Author to whom any correspondence should be addressed.E-mail: robinson.inj@lbl.gov, cdkoven@lbl.gov, wjriley@lbl.gov, rgknox@lbl.gov and jchambers@lbl.gov**Keywords:** tropical biomass, tropical productivity, biomass turnover time, earth system modelsSupplementary material for this article is available [online](#)**Abstract**

A significant fraction of anthropogenic CO₂ emissions is assimilated by tropical forests and stored as biomass, slowing the accumulation of CO₂ in the atmosphere. Because different plant tissues have different functional roles and turnover times, predictions of carbon balance of tropical forests depend on how earth system models (ESMs) represent the dynamic allocation of productivity to different tree compartments. This study shows that observed allocation of productivity, biomass, and turnover times of main tree compartments (leaves, wood, and roots) are not accurately represented in Coupled Model Intercomparison Project Phase 5 ESMs. In particular, observations indicate that biomass saturates with increasing productivity. In contrast, most models predict continuous increases in biomass with increases in productivity. This bias may lead to an over-prediction of carbon uptake in response to CO₂ or climate-driven changes in productivity. Compartment-specific productivity and biomass are useful benchmarks to assess terrestrial ecosystem model performance. Improvements in the predicted allocation patterns and turnover times by ESMs will reduce uncertainties in climate predictions.

1. Introduction

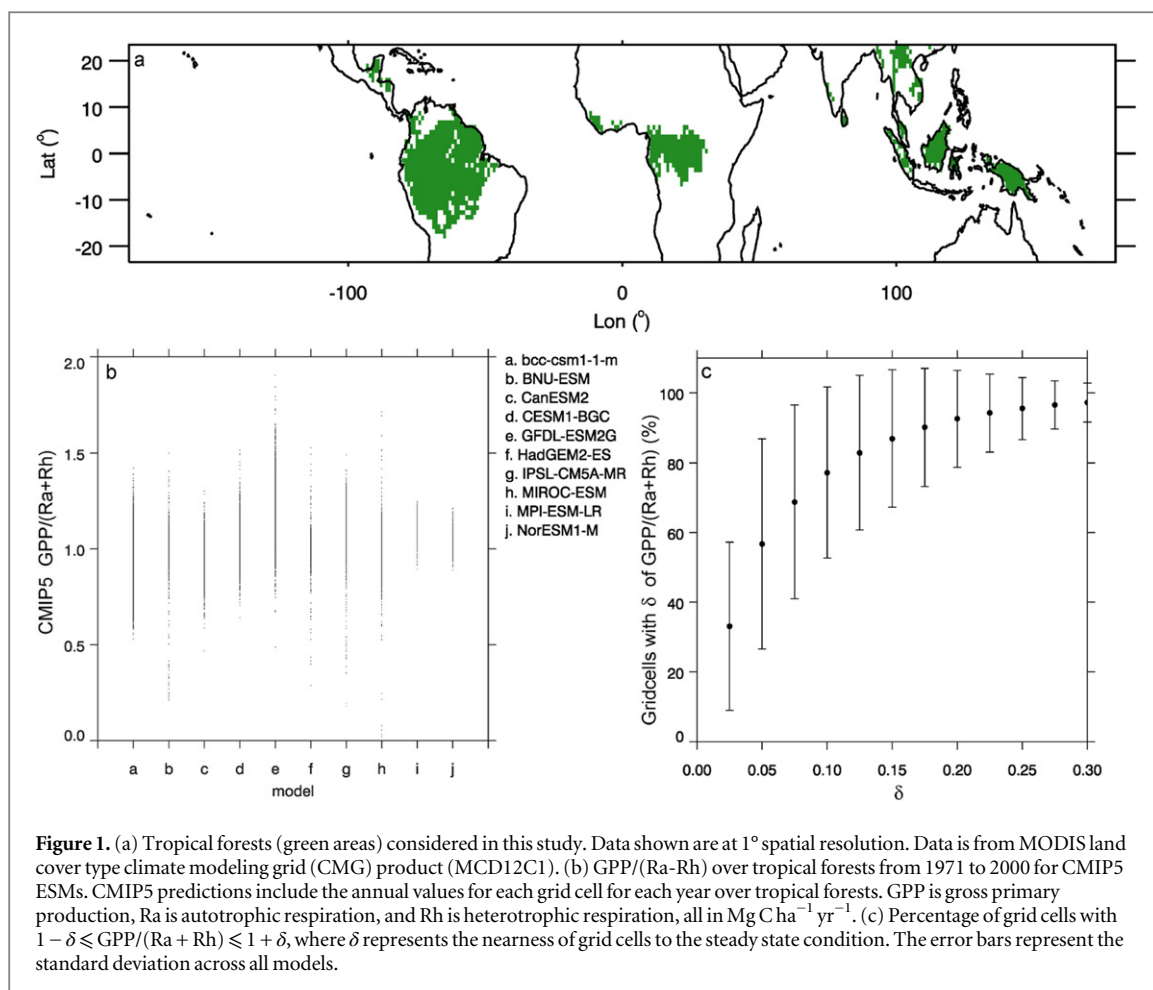
Due to anthropogenic activities, atmospheric CO₂ concentrations have increased from ~280 ppm in 1750 (IPCC 2013) to current levels of ~400 ppm (Tan and Keeling 2014), with increases projected to continue (IPCC 2013). Concomitant to increases in atmospheric CO₂ concentrations is an increase in air temperatures (IPCC 2013). Tropical forests assimilate a large amount of atmospheric CO₂, accounting for ~34% (42 PgC yr⁻¹) (Beer *et al* 2010) of total global terrestrial gross primary production (GPP). Part of this carbon is lost to the atmosphere during metabolism (autotrophic respiration, Ra) and the remaining flux (net primary production, NPP) in tropical forests represent ~35% (22 PgC yr⁻¹) of the total global NPP (Pan *et al* 2013, Fernandez-Martinez *et al* 2014). Most NPP is stored as biomass and tropical forests contain

about 66% (~262 PgC) (Pan *et al* 2013) of global terrestrial biomass, equivalent to ~1.7 times the terrestrial carbon sink since 1850 (Boden *et al* 2010, Le Quére *et al* 2014), contributing to reduce global warming effects (IPCC 2013). Therefore tropical forests are key components of the carbon cycle and an important regulator of global climate.

NPP and biomass are fundamental variables of the global carbon cycle representing net absorption and net storage of carbon respectively. At steady state, forest biomass is the balance between productivity and losses (characterized by turnover times) in tree compartments (Malhi *et al* 2011):

$$\text{Biomass}_i = \text{NPP}_i \times \tau_i, \quad (1)$$

where i = leaves, wood, and roots (i.e., the main tree compartments) and τ_i is the turnover time of individual compartments (total biomass is the sum of all



biomass compartments). The mechanisms that control the allocation of productivity and biomass in trees are not fully understood (Chambers and Silver 2004, Cleveland *et al* 2011, Malhi *et al* 2011, De Kauwe *et al* 2014, Michaletz *et al* 2014). However, in tropical forests, patterns of productivity allocation (Aragao *et al* 2009, Cleveland *et al* 2011, Malhi *et al* 2011), biomass allocation (Poorter *et al* 2012, Fernandez-Martinez *et al* 2014, Mitchard *et al* 2014), biomass turnover time (Stephenson and van Mantgem 2005, Malhi *et al* 2011, Stephenson *et al* 2011, Malhi 2012, Carvalhais *et al* 2014), and covariation of productivity and biomass (Keeling and Phillips 2007, Malhi *et al* 2011, Pan *et al* 2011, Malhi *et al* 2015) have been observed. These observations provide valuable constraints on terrestrial carbon cycle models, as demonstrated here.

The latest versions of earth system models (ESMs; global models which couple the physical climate system with the carbon cycle (Bonan 2008, Shao *et al* 2013, Friedlingstein *et al* 2014) are part of the fifth phase of the Coupled Model Intercomparison Project (CMIP5) (Taylor *et al* 2012) and allow for an integrative study of the Earth system. These models predict the allocation of biomass and productivity. Thus, how CMIP5 ESMs reproduce observed allocations and biomass–productivity relationships in tropical ecosystems can be used to test models and provide specific

suggestions for model improvements. This work, therefore, has the following objectives:

- (i) To compare observations and CMIP5 ESM predictions of allocations of productivity and biomass, and turnover times of main tree compartments (leaves, wood, and roots).
- (ii) To determine whether CMIP5 ESMs reproduce the observed spatial patterns of NPP and biomass in tropical forests.

2. Data and methods

2.1. Study area

This study focuses on tropical forests (180°W–180°E, 23.43°S–23.43°N) (figure 1(a)). Tropical forest areas were selected using the moderate resolution imaging spectroradiometer (MODIS) land cover type climate modeling grid (CMG) product (MCD12C1 Version 051, 0.05°, available at <https://lpdaac.usgs.gov/>) (Friedl *et al* 2010) for the year 2001. The International Geosphere-Biosphere Program global vegetation classification (Loveland and Belward 1997) of evergreen broadleaf forests was used to identify tropical forests. A conservative mask of tropical forested areas was created by considering only pixels with good quality

(flag 0 in quality control files), forest land cover greater than 80% and reliability (assessment) greater than 85%. This forest mask was applied to all model simulations analyzed here, and correspond to CMIP5 cells with $\geq 40\%$ of forest cover (figure S1, supplementary data).

2.2. CMIP5 models

Monthly fields from historical simulations for the period 1971–2000 from 22 CMIP5 ESMs models (available at <http://cmip-pcmdi.llnl.gov/>) were used in this study (table S1). Since models from the same institution produce similar results (Masson and Knutti 2011, Knutti *et al* 2013) we chose one model per institution to present and discuss: bcc-csm1-1 m (hereinafter referred as bcc), BNU-ESM (BNU), CanESM2, CESM1-BGC (CESM1), GFDL-ESM2G (GFDL), HadGEM2-ES (HadGEM2), MIROC-ESM (MIROC), MPR-ESM-LR (MPI), and NorESM1-M (NorESM1). Results for the 22 models are presented in supplementary data (see section 3).

CMIP5 ESMs historical simulations are coupled simulations where the increase of atmospheric CO₂ affects both the climate and the carbon cycle components of the models, and can be compared directly with current observations (Taylor *et al* 2012). In CMIP5 models, total biomass is represented by cVeg and the biomass in the main tree compartments are cLeaf, cWood, and cRoot (coarse + fine roots). Net primary productivity is identified as npp which is disaggregated into nppLeaf, nppWood, and nppRoot. For simplicity, total productivity will be referred to as NPP (MgC ha⁻¹ yr⁻¹) and total biomass as cVeg (MgC ha⁻¹). The ensemble members available at the time of this study per each CMIP5 model were averaged and monthly data integrated annually (January to December). The annual data per each CMIP5 model were used in our analyses. The ratio of nppLeaf, nppWood, and nppRoot, to NPP and the ratio of cLeaf, cWood, and cRoot to cVeg were compared with observations. Ratios between predicted fluxes and pools (nppLeaf/cLeaf, etc) were compared with observed turnover times calculated in an analogous manner.

The CMIP5 ESM predicted association between NPP and cVeg were presented and discussed with respect to observational studies. We explored quadratic ($cVeg = a + b \times NPP + c \times NPP^2$) and linear ($cVeg = a + b \times NPP$) models to explain predicted NPP versus cVeg relationships. The MPFIT fitting package (<http://purl.com/net/mpfit>) (Markwardt 2009) for the interactive data language (IDL, Exelis Inc., McLean, VA) was used for this task. If the linear and quadratic models had statistically similar variance (significance level of 95%), determined by the F-test (Wilks 2006), then the linear model was preferred over the quadratic model because fewer parameters were required (Wilks 2006). If the models had statistically

different variance, then the model with lower fitting errors (lower χ^2 Wilks 2006) was preferred. A visual inspection was performed to complement this comparison.

In CMIP5 ESMs, disturbances such as fire and drought can produce dramatic departures from steady state conditions. CMIP5 ESMs with a fire module include CESM1, IPSL, MPI, and GFDL. Under steady state conditions, carbon inputs (GPP) balance outputs (Ra, and soil heterotrophic respiration, Rh), and equation (1) is valid. To ensure that grids cells are not disturbed forests the following condition was considered: $1 - \delta \leq GPP/(Ra + Rh) \leq 1 + \delta$. The selection of δ must be small to better approximate a steady state condition. For simplicity we selected a common value of δ for all models analyzed.

2.3. NPP and biomass data

Mean NPP value for lowland tropical forests was estimated to be 11.86 ± 2.47 MgC ha⁻¹ yr⁻¹ (mean \pm SD) (Malhi *et al* 2011) with a range from 8.4 to 29.8 MgC ha⁻¹ yr⁻¹ (Cleveland *et al* 2011) (table S2). This mean NPP agrees with another recent tropical estimate (11.08 ± 1.2 MgC ha⁻¹ yr⁻¹, Cleveland *et al* 2015). The observationally-based fractional allocation of NPP to leaves, wood, and roots was $34 \pm 6\%$, $39 \pm 10\%$, and $27 \pm 11\%$, respectively (Malhi *et al* 2011). However, these authors considered only fine roots (in CMIP5 models nppRoot includes coarse and fine roots). Coarse root NPP is difficult to assess but represents a small fraction (4%) of total NPP (Clark *et al* 2001). Similarly, fine root production is not measured directly and observational assessments have serious limitations (Lukac 2012). Since estimated values of coarse root NPP are in the range of the uncertainties of NPP allocation (Malhi *et al* 2011) we did not attempt to correct these values. Therefore, the fractional allocation of NPP to nppRoot was directly compared with the observed value. Mean tropical biomass was taken to be 144 ± 54 MgC ha⁻¹ (Saatchi *et al* 2011) (<ftp://www-radar.jpl.nasa.gov/projects/carbon/datasets/>), with a range from 50 and 350 MgC ha⁻¹ (Malhi *et al* 2011, Saatchi *et al* 2011, Baccini *et al* 2012, Lewis *et al* 2013). The mean biomass agrees well with the value of 151 MgC ha⁻¹ found by Baccini *et al* (2012) (table S2). Biomass was divided into leaves, stems, and roots as $4 \pm 2\%$, $78 \pm 4\%$, $18 \pm 2\%$, respectively (Poorter *et al* 2012, Fernandez-Martinez *et al* 2014). We combined equation (1), the mean \pm SD values of biomass and productivity (taken as representative of tropical forests), and allocation fractions (to leaves, wood, and roots) to calculate turnover times (yr) (using a Monte Carlo simulation with 10 000 iterations) and compare with independent observationally-based values.

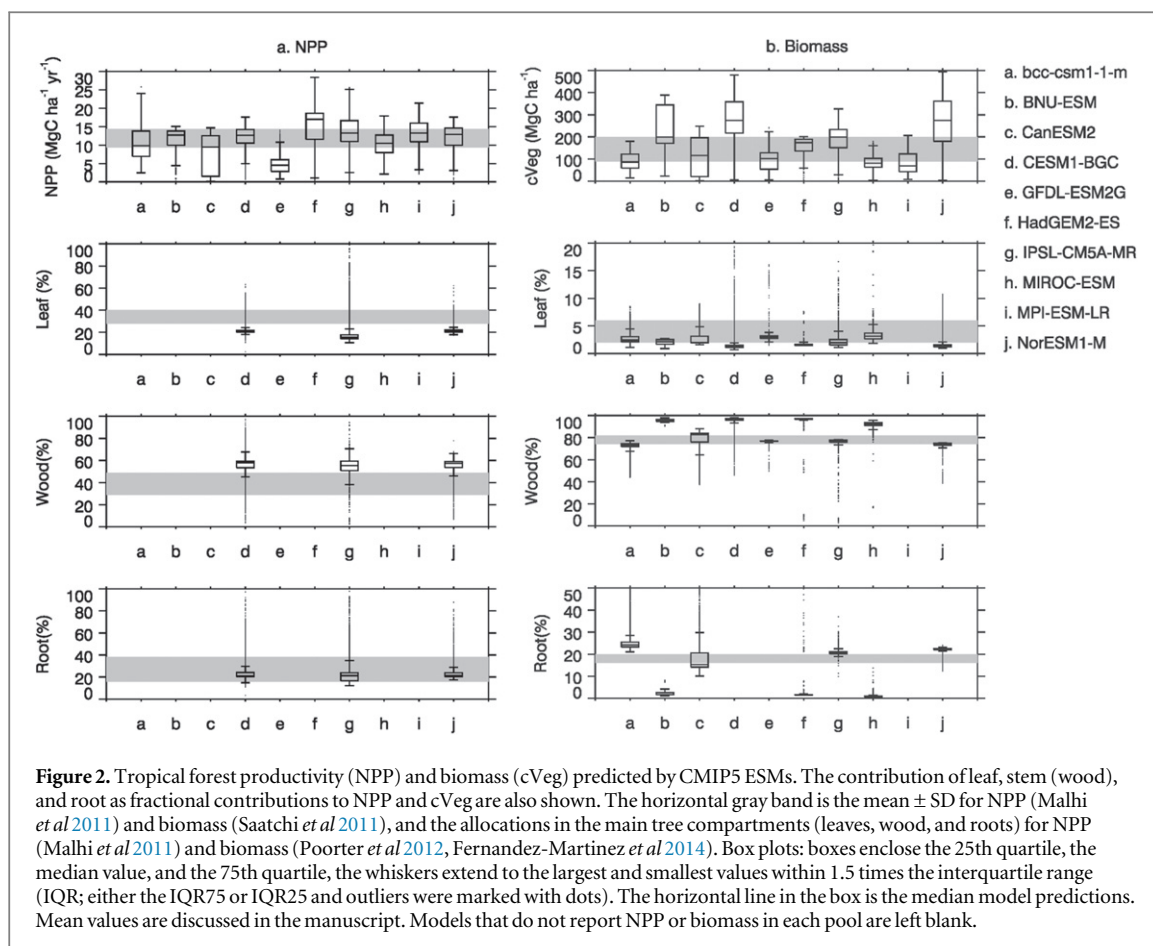


Figure 2. Tropical forest productivity (NPP) and biomass (cVeg) predicted by CMIP5 ESMs. The contribution of leaf, stem (wood), and root as fractional contributions to NPP and cVeg are also shown. The horizontal gray band is the mean \pm SD for NPP (Malhi *et al* 2011) and biomass (Saatchi *et al* 2011), and the allocations in the main tree compartments (leaves, wood, and roots) for NPP (Malhi *et al* 2011) and biomass (Poorter *et al* 2012, Fernandez-Martinez *et al* 2014). Box plots: boxes enclose the 25th quartile, the median value, and the 75th quartile, the whiskers extend to the largest and smallest values within 1.5 times the interquartile range (IQR; either the IQR75 or IQR25 and outliers were marked with dots). The horizontal line in the box is the median model predictions. Mean values are discussed in the manuscript. Models that do not report NPP or biomass in each pool are left blank.

3. Results

Most CMIP5 tropical forest were close to steady state (figure 1(b)), but departures from this condition exist. Figure 1(c) shows that between 10% and 60% of data per model satisfy $1 - \delta \leq \text{GPP}/(\text{Ra} + \text{Rh}) \leq 1 + \delta$ for $\delta = 0.025$. $\delta = 0.1$ encompassed most of the data. In this study we choose $\delta = 0.1$ as the cut off for steady-state conditions, so that only cells satisfying $0.9 \leq \text{GPP}/(\text{Ra} + \text{Rh}) \leq 1.1$ were used in the following analyses. For the purposes of this study, the selection of δ had little to no effect on our results as observed in all models studied (figure S2).

Mean NPP model predictions varied from $4.8 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (GFDL) to $15.4 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (HadGEM2), and BNU, CESM1, and NorESM1 simulated values (average of $11.7 \text{ MgC ha}^{-1} \text{ yr}^{-1}$), close to observations (figure 2, and table S3). CESM1, IPSL, and NorESM1, corresponding to two distinct land models (CLM4 and ORCHIDEE, table S1), provided the components of NPP allocated to leaves, wood, and roots. These models allocated NPP to (1) roots consistent with observations; (2) wood higher than observations (56% versus 39%); and (3) leaves lower than observation (19% versus 34%). On average, predicted nppLeaf , nppWood , and nppRoot represented $19\% \pm 2\%$, $56\% \pm 1\%$ and $21\% \pm 1\%$ of NPP.

The models that better reproduced mean NPP (BNU, CESM1, and NorESM1) performed worse for mean biomass (cVeg) (figure 2(b), table S3), simulating the highest values (average of $\sim 257 \text{ MgC ha}^{-1}$) among the CMIP5 models we analyzed. HadGEM2 (157 MgC ha^{-1}) and IPSL (183 MgC ha^{-1}) predicted biomass values close to observations. The bcc, MIROC, and MPI predictions were the lowest among models. With respect to the allocation of biomass in the main tree compartments, all models predicted a smaller fraction of cVeg allocated to cLeaf than observed, a feature that may be related to the lower NPP allocated to this compartment (figure 2(a)). Also, all models showed a large fraction of cVeg allocated to cWood consistent with observations, but there were several differences. Relative to observations, the fraction of biomass in wood was high in BNU, CESM1, HadGEM2, and MIROC; this fraction was low in the bcc model. The higher wood allocation relative to observations in productivity and biomass in models using CLM4 could explain higher total biomass (top panel figure 2(b)). Finally, the fraction of biomass in roots varied among models. cRoot was over predicted in bcc and NorESM1 models, and under predicted in BNU, HadGEM2, and MIROC, relative to observations. The fraction of biomass in cRoot simulated by CanESM2 and IPSL were close to observations. Two contrasting patterns in the fractions of biomass in

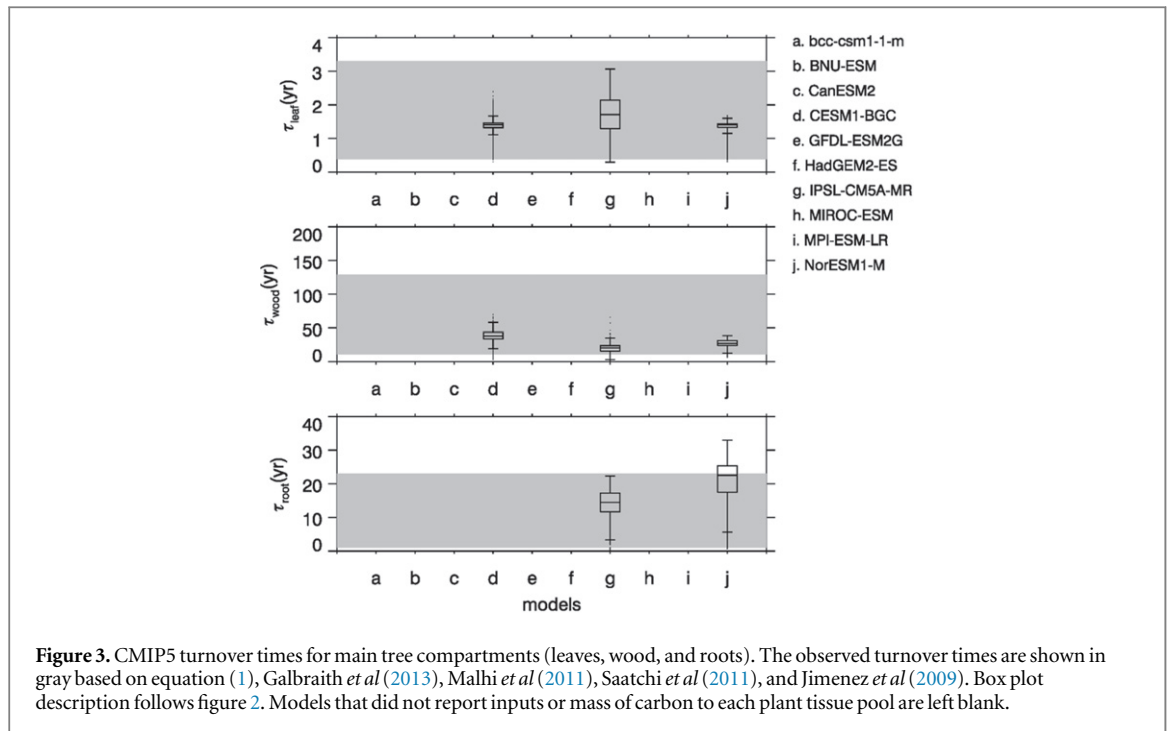


Figure 3. CMIP5 turnover times for main tree compartments (leaves, wood, and roots). The observed turnover times are shown in gray based on equation (1), Galbraith *et al* (2013), Malhi *et al* (2011), Saatchi *et al* (2011), and Jimenez *et al* (2009). Box plot description follows figure 2. Models that did not report inputs or mass of carbon to each plant tissue pool are left blank.

wood and root pools are evident: a set of models with close to zero root biomass and close to 100% wood biomass, and a set of models with $\sim 20\text{--}30\%$ root and $70\text{--}80\%$ wood, suggesting that the definition of wood and roots is inconsistent across the CMIP5 models (some labeling coarse roots as wood and some labeling coarse roots as roots). Although CMIP5 ESMs also provide biomass for other minor tree pools, cLeaf, cWood, and cRoot encompass the dominant proportion of total biomass, representing on average 1% , $85\% \pm 10\%$, and $12\% \pm 10\%$ of cVeg.

We found that τ_{leaf} varied between 0.39 and 3.3 yr, and comparable with observed values (1 yr) in tropical forests (Chave *et al* 2010). τ_{wood} varied between 11 and 54 yr. Using tropical forests plots Galbraith *et al* (2013) found τ_{wood} between 23 and 129 yr and a median of 50 yr that reflect the high diversity of taxa in tropical forests. In this study we considered τ_{wood} between 11 and 129 yr. Finally, τ_{root} varied between 3 and 23 yr, values that are larger than site estimates (1 to 7 yr) (Jimenez *et al* 2009). This difference may be explained by the fact that measurements of root turnover are achieved by indirect means resulting in high uncertainties (Lukac 2012). Estimates using ^{14}C to estimate fine-root turnover in temperate trees has indicated that a spectrum of turnover times exist, with two dominant peaks of ~ 1 and ~ 10 yr (Riley *et al* 2009, Gaudinski *et al* 2010). The range of τ_{root} from 1 to 23 yr was considered in this study. Figure 3 shows these turnover times compared with turnover time obtained from models. For the CMIP5 ESMs that provided sufficient information to calculate these turnover times, the mean leaf lifetime was 3 to 6 months longer than the mean observed value ($\tau_{\text{leaf}} = 1$ yr). The predicted turnover time of woody biomass was 10–30

yr shorter than the median of 50 years observed in tropical forests, and roots had mean turnover times about 50% larger than the mean value (9 yr, but see Jimenez *et al* 2009). NorESM1 models used the same base land model (CLM4) as used in CESM1. However, numerous physical parameterizations were changed in the CLM version used by NorESM1 (Bentsen *et al* 2013), potentially explaining the differences between these models.

Three patterns of NPP versus cVeg emerged from the CMIP5 models (figure 4, and figure S3): (A) concave up: CESM1, MPI and NorESM1; (B) linear: bcc, BNU, CanESM2, GFDL, IPSL and MIROC; and (C) concave down: HadGEM2. CESM and NorESM1 use the same land model (CLM4) and therefore their NPP–cVeg patterns were very similar. In CLM4, the fractional allocation to wood increases as a function of increasing NPP (Thornton and Zimmermann 2007), which is responsible for the concave-upwards curve. The HadGEM2 models produced the only simulations with a saturating relationship that appears to arise from the TRIFFID vegetation dynamics underlying HadGEM2. In TRIFFID the allocation to woody growth for range expansion of a given PFT (plant functional type) decreases when that PFT occupies a large fraction of a cell, resulting in a density-dependent vegetation turnover time. In addition, HadGEM2 NPP and cVeg maps (figure S4) showed that $\text{NPP} > \sim 15 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ and $\text{cVeg} < \sim 190 \text{ MgC ha}^{-1}$ were observed contouring the borders of tropical forests. These forest grid cells included also grasses (figure S5) that are highly productive and have low biomass which may partially explain the decrease of cVeg with an increase in NPP for $\text{NPP} > \sim 15 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (and which is a mechanism different than

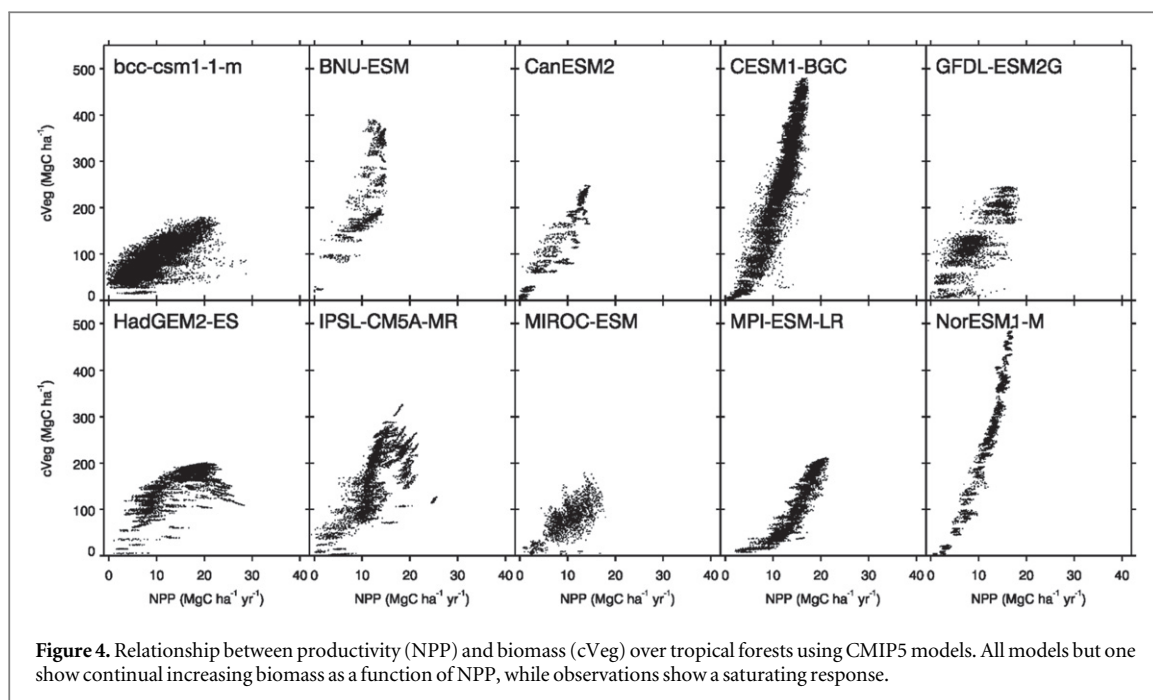


Figure 4. Relationship between productivity (NPP) and biomass (cVeg) over tropical forests using CMIP5 models. All models but one show continual increasing biomass as a function of NPP, while observations show a saturating response.

represented in the observed benchmark relationship, which only considers trees).

4. Discussion

A full understanding of processes that govern allocation remains elusive. Despite this limitation, models attempt to reproduce allocation using schemes that vary between models and depend on the PFT. CMIP5 models calculate allocation to leaves, wood, and roots using (1) allometric relationships and leaf area index, LAI, (as in AVIM2 in bcc, JULES in HadGEM2, table S1); (2) NPP (CLM4 in CESM1 and NorESM1, JSBACH in MPI). The land model used by BNU is the CoLM that is based on previous versions of CLM4), (3) allometry and resource availability (as CETEM in CanESM and ORCHIDEE in IPSL), (4) environmental conditions at the tree level (as in SEIB-DGVM in MIROC), and (5) tree height (as LM3.0 in GFDL). Our results suggest that the schemes used by CMIP5 models did not accurately represent the observed allocations in leaves, wood, and roots. Additionally, the strategies used to calculate allocation in the CMIP5 models have advantages and disadvantages. For instance, models based on the allometric approach lack the inherent ecosystem adaptation component to predict the effects of environmental variability and climate change (Franklin *et al* 2012).

Model predicted NPP and biomass values agreed well with the observational range but models seem to be capable of reproducing either the observed mean NPP or the observed mean biomass but not both. This pattern is likely related to the embedded model schemes that calculate NPP and biomass allocations. Models whose allocations are based on NPP better

reproduced the observed mean NPP (BNU, CESM1 and NorESM1) and models using allometry better reproduced the observed mean biomass (HadGEM2 and IPSL). The models that report pool-specific allocation consistently overestimate the fraction of productivity allocated to wood, and underestimate the fraction of productivity allocated to leaves, when compared with observations. The allocations to root productivity and leaf biomass appear to be close to observations across most CMIP5 models. CMIP5 models have fractional biomass in leaves at the low end of the mean observational range, and their fractional biomass in roots and wood show a bimodal pattern that suggests an inconsistent definition of coarse roots as either roots or wood between the models. CMIP5 woody parts contain the largest fraction of biomass in agreement with observations but have faster turnover time in that component (10–30 yr faster than the observed median of 50 yr), resulting in predictions of higher productivity or lower biomass. Our analysis was limited due to lack of available model data for the main compartments of NPP and biomass. We suggested that all ESM's participating in future inter-comparison projects include and consistently define the main pools (leaves, wood, and root) of productivity and biomass to better understand their predictions.

Models predict a continuous increase in biomass with increased productivity. For instance, CLM4 adopts a continuous increase in the fraction of carbon allocated to wood with increases in NPP (Oleson *et al* 2010). However observational studies show a different pattern. Keeling and Phillips (2007) found that biomass saturates at high productivity values (figure S6), and recent studies confirm this pattern (Malhi *et al* 2011, Stephenson *et al* 2011, Malhi 2012). The saturation of biomass to high productivity occurs

because highly productive forests have short residence times and their tree species prioritize fast growth that results in low wood density and therefore low biomass (Malhi *et al* 2015). The fact that ESMs do not reproduce the observed saturation response of biomass at high NPP raises a critical question about model predictions of carbon cycle responses to global change: Do the same saturating conditions hold for the higher productivity environments expected as a result of elevated CO₂ conditions (Norby *et al* 2005) as for the current spatial patterns? If so, and since the models do not represent the mechanisms behind this saturating response, we expect the models will likely over predict carbon uptake in response to CO₂ or climate-driven changes in productivity. These functionally incorrect responses imply model structural uncertainty associated with vegetation tradeoffs.

Biomass per unit area was found to be larger in Asia, followed by Africa and then Amazonia (Lewis *et al* 2013, Slik *et al* 2013, Banin *et al* 2014). IPSL and CanESM2 appears to capture this regional pattern (figure S7). However, a close observation revealed that in CanESM2 lower values of biomass in Amazonia were produced by extremely (and unrealistically) low values of biomass over a large fraction of Amazonia (figure S4). In addition, observational studies show that Northwestern Amazonia is the most productive area in the Amazon (Malhi and Davidson 2009, Cleveland *et al* 2011, Malhi *et al* 2011) and the most diverse (ter Steege *et al* 2013), but it also has lower biomass due to faster turnover time (Aragao *et al* 2009, Malhi and Davidson 2009, Quesada *et al* 2012, Galbraith *et al* 2013). CMIP5 models were consistent with observations in predicting higher NPP in Northwestern Amazonia relative to the Amazon basin but inconsistent with observations by simulating higher biomass in this region (figure S4). The models' limited ability to reproduce the decrease of cVeg at high NPP raises concerns about predictions in areas with high productivity. It also raises concerns about carbon stocks projections associated with projected increase in productivity due increase in atmospheric CO₂ (Wieder *et al* 2015).

Observational data used to benchmark the CMIP5 ESMs are of great value but contain their own uncertainties (Malhi *et al* 2011, Samanta *et al* 2011, Mitchell *et al* 2014, Cleveland *et al* 2015, Malhi *et al* 2015). Yet, patterns in productivity and biomass emerge that models were unable to capture and that likely affect model predictions. For instance, to be comparable with observation models need to increase NPP allocation to leaves that in turn may increase LAI and affect climate predictions through changes in albedo, evapotranspiration, and CO₂ surface fluxes (Negrón-Juárez *et al* 2007, 2009, Myneni *et al* 2007, Bonan 2008). The continuous increase of biomass with increased NPP in all models suggest, for instance, that mortality mechanisms are inaccurate in models. Improved representation of mortality is needed, since tree

mortality has a large impact on carbon storage (Delbart *et al* 2010, Malhi 2012, Stephenson *et al* 2014, Malhi *et al* 2015). For instance, an important form of tree mortality in Amazonia are windthrows (Nelson *et al* 1994, Chambers *et al* 2013), that are not represented in CMIP5 ESMs, but have a strong effect on forest dynamics and composition (Negrón-Juárez *et al* 2010, Negrón-Juárez *et al* 2011, Chambers *et al* 2013, Holm *et al* 2014, Marra *et al* 2014).

5. Conclusion

The CMIP5 models used in this study did not reproduce the observed allocation of productivity, biomass, and turnover time in the main tree compartments (leaves, wood, and roots) in tropical forests. All models systematically predict an increase in biomass with an increase in NPP in the lower NPP range observed in tropical forests. Observations also suggest a limit for this increase, a pattern not simulated by the models. The models inability to reproduce the observed patterns of allocation of NPP and biomass raises concerns about climate projections, in particular whether the limitations to vegetation accumulation under high productivity conditions also hold for the responses of forest vegetation carbon stocks under future global change. Regional differences of predicted biomass and NPP were observed across models. Model improvements in representing observed allocations of productivity and biomass in the main tree compartments may lead to changes in climate predictions.

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