



Spatial biases reduce the ability of earth system models to simulate soil heterotrophic respiration fluxes

Bertrand Guenet^{1,*}, Jérémie Orliac¹, Lauric Cécillon^{1,2}, Olivier Torres³, Laura Sereni⁴, Philip A. Martin⁵, Pierre Barré¹, Laurent Bopp³

5

¹ Laboratoire de Géologie, Ecole normale supérieure, CNRS, IPSL, Université PSL, 24 Rue Lhomond, 75005 Paris, France

² Laboratoire ECODIV, Univ. Normandie, UNIROUEN, INRAE, Rouen, France.

³ LMD-IPSL, Ecole Normale Supérieure, Université PSL, CNRS, Ecole Polytechnique,
10 Sorbonne Université, Paris, France.

⁴ INRAE, AgroParisTech, Université Paris-Saclay, UMR1402 ECOSYS, Ecotoxicology Team, 78026, Versailles, France.

⁵ Basque Centre for Climate Change (BC3), Edificio sede no 1, planta 1, Parque científico UPV/EHU, Barrio Sarriena s/n, 48940, Leioa, Bizkaia, Spain.

15 *Correspondence to:* Bertrand Guenet (guenet@geologie.ens.fr)

Abstract. Heterotrophic respiration (Rh) is, at a global scale, one of the largest CO₂ fluxes between the earth's surface and atmosphere and may increase in the future. Yet, the capacity of Earth System Models (ESMs) to reproduce this flux has never been evaluated, causing uncertainty in resulting CO₂ flux estimates. In this study, we combine recently released observational data on Rh and ESM simulations to evaluate, for the first time, the ability of 13 ESMs to reproduce Rh. Only
20 four of the 13 tested were able to reproduce the total Rh flux but spatial analysis underlined important bias compensation. We observed that mean annual precipitation was the most important driver explaining the difference between ESM simulations and observation-derived product of Rh with higher bias between ESM simulations and Rh products where precipitation was high. Based on our results, next-generation ESMs should focus on improving the response of Rh to soil moisture.



25 1 Introduction

Stocks of soil organic carbon are estimated to represent around three times the amount of carbon in the atmosphere (Scharlemann et al., 2014). This soil carbon is used as a substrate by soil microorganisms to obtain their energy and feed their metabolism, which account for the majority of heterotrophic soil organism biomass. Annual fluxes that result from the respiration of these heterotrophic organisms (hereafter referred to as heterotrophic respiration) are estimated (Ciais et al., 2021; Hashimoto et al., 2015; Konings et al., 2019; Warner et al., 2019) to be five times higher than annual anthropogenic emissions (Friedlingstein et al., 2020) and roughly similar to annual terrestrial net primary production (Zhao et al., 2005). Thus, due to the size of fluxes relating to heterotrophic respiration, even minor changes in soil organic carbon dynamics can lead to significant impacts on carbon feedbacks and, ultimately, on climatic changes. As a result, modification of soil organic carbon stocks due to human activities is considered to be an important driver of future climate trajectories (Chabbi et al., 2017).

Despite the importance of heterotrophic fluxes, they have not been well characterized and incorporated into earth system models (ESMs), which aim to simulate the most important drivers of the earth's climate system. Although the carbon fluxes of oceans and plants have been well characterized and incorporated into earth system models (Luyssaert et al., 2018; Séférian et al., 2020) this is not true of fluxes resulting from heterotrophic respiration – and as such, these represent a key source of uncertainty regarding carbon flux. Given the importance of carbon exchange between the earth's surface and atmosphere as a driver of atmospheric CO₂ it is vital that such exchanges are accurately represented in earth system models.

Assessing how accurately current ESMs reproduce the fluxes associated with heterotrophic respiration is therefore of major importance. Until now, it was not possible to undertake a robust spatial assessment because of the lack of observation-derived gridded products of Rh. In recent years, new gridded products derived either from (i) upscaling of local observation or (ii) calculations using atmospheric inversions and satellite observations have filled this gap. These products provide the opportunity to evaluate the simulations of ESMs used within the Coupled Model Intercomparison Project Phase 6 (CMIP6) against observation-derived products for heterotrophic respiration. CMIP is a key initiative which aims to compare current ESMs and is a central element of national and international assessments of climate change (Masson-Delmotte et al., 2021).

In this study we have two major aims:

1. Compare predictions of the total flux of heterotrophic respiration from 13 earth system models with three recent gridded products of heterotrophic respiration derived from observations and identify the spatial biases of heterotrophic respiration in the models.
2. Identify the major drivers of the heterotrophic respiration bias in earth system models to propose way of improvement for the next generation of earth system models.



2 Materials and Methods

2.1 Earth System Models simulations.

In this study, we used the model outputs from the 6th Coupled-Model Intercomparison Project (CMIP6) (Eyring et al., 2016) which coordinates global climate model simulations of the past, current, and future climate. CMIP6 proposes historical simulation spanning from 1850 to 2014. Historical simulations are driven from an initial point chosen in control integration (*piControl*). We chose to use the latest CMIP6 results for basic initial state (r1i1p1f1). We choose outputs from thirteen ESMS that provide heterotrophic respiration fluxes (BCC-CSM2-MR, BCC-ESM1, CanESM5, CESM2, CNRM-ESM2-1, E3SM-1-1-ECA, IPSL-CM6A-LR, MIROC-ES2L, MPI-ESM1-2-LR, NorCPM1, NorESM2-LM, SAM0-UNICON and UKESM1-0-LL). The variable used is "rh" corresponding to the total heterotrophic respiration on land. We computed annual average over the 1990-2010 period which corresponds to the period in which most of the observations in the global Soil Respiration Database (Bond-Lamberty and Thomson, 2010) v3.0 were made, which were used to derived two observation products we used.

2.2 Observation-derived products.

In this study we used three observation derived products (Hashimoto et al., 2015; Konings et al., 2019; Warner et al., 2019). In Warner et al. (2019), the authors predicted annual soil respiration and associated uncertainty across terrestrial areas at a resolution of 1 km using a quantile regression forest algorithm trained with observations from the global Soil Respiration Database (Bond-Lamberty and Thomson, 2010) v3.0 (commit number 651770 in GitHub, <https://github.com/bpbond/srdb>) spanning from 1961 to 2011 but mostly after 1990. Then they deduced Rh from the soil respiration using two different methods (Bond-Lamberty et al., 2004; Subke et al., 2006). They therefore proposed two Rh maps derived from a unique mean map of Rs from quantile regression forest model. Here, we decided to use the mean of two approaches as a reference for Warner et al. (2019) Rh results. The second product we used (Hashimoto et al., 2015) called here Hashimoto et al. (2015) is also based on the Soil Respiration Database (Bond-Lamberty and Thomson, 2010) v3.0 but in this case they derived the Rh flux using a climate-driven model of soil respiration derived from the Raich's model (Raich et al., 2002). They provided a 0.5° resolution product at a monthly step time between 1965 and 2012. In our case, we used the yearly average over the period. The third product used (Konings et al., 2019) called here Konings et al. (2019) estimated Rh as a residual remote-sensing data exploiting recent advance in carbon-flux estimations. In contrast with the two other products which can be considered as bottom up, the Konings et al., (2019) product propose a top-down approach combining net ecosystem productivity estimates from atmospheric inversions with an optimally scaled gross primary productivity dataset derived from satellite observations. Rh is then derived using the CARbon DAta MOdel fraMework, (CARDAMOM). Their result is a monthly evaluation of Rh, between 2010-01 and 2012-12, at a resolution 4°×5°.

2.3 Data treatment and regriding.



All the ESMs outputs and products were not at the same resolution. Thus, we needed to choose a reference for map-grid
90 resolution. The coarser resolution was from Konings et al. (2019)'s product with a $4^{\circ} \times 5^{\circ}$ resolution grid. Degrading every
Rh map at such resolution would be a substantial loss of information. Thus, we increased the resolution of those datasets and
decreased the very fine scale maps to an arbitrary reference corresponding to the CNRM-ESM2-1 model which runs at 0.7°
resolution. We chose to set the reference at the maximum resolution available among CMIP6's ESMs predicting Rh. We
used the common regriding routine `cdo remapdis` (`nco` module) that performs regriding by distance-weighted average
95 remapping and conserve latitudinal and longitudinal means. To avoid coastal pixels encroaching into oceans, we weighted
each pixel by its proportion of land. The sum of Rh over the lands was compared before and after regriding to ensure that it
was conservative.

2.4 Comparison between models' outputs and heterotrophic respiration products.

100 To estimate the ability of the CMIP6's model to reproduce soil heterotrophic respiration, we first compared the global flux
summed over all the grid cells and averaged over 1990-2010 period in Pg C yr^{-1} . We also compared the Rh maps after
regriding averaged over the 1990-2010 period. We also performed latitudinal and longitudinal means calculus including
oceanic zero-values. Secondly, we wanted to assess spatial bias distribution. Therefore, we i) compare CMIP6 model
average with observation products and ii) compare each CMIP6 models with observation products. Thus, we first
105 represented the model average (over the period 1990-2010) and all the observation derived products on a same figure with
their associated latitudinal and longitudinal means. We also calculated the 25th and 75th quantiles of latitudinal and
longitudinal CMIP6 model means. Then, we computed the difference for each single CMIP6 models with the median of the
three observation products.

110 2.5 ESM's model residual analysis.

We defined here the ESM's model residuals as median of the difference between each single CMIP6's model output and the
observation-based products median calculated for each grid cell. We proceed with a two-step methodology. First, we
compared several linear generalized least square models with different spatial structures (gaussian, exponential, spherical,
linear or rational (gls package)) and without spatial structures. Based on AIC values we selected the rational quadratic spatial
115 correlation structure that had the smallest AIC values for the second step of the analysis. Then, we used generalized additive
mixed model with ESM's model residuals as variable to explain and mean annual temperature (MAT), mean annual
precipitation (MAP), observation derived SOC, ESM's model residuals on NPP and lithology as predictors variables. MAT
and MAP are derived from the Global Soil Wetness Project Phase 3 (GSWP3) reanalysis ([http://hydro.iis.u-
tokyo.ac.jp/GSWP3/](http://hydro.iis.u-tokyo.ac.jp/GSWP3/) last access: April 5 2022). SOC was taken from the Soilgrid250m product(Hengl et al., 2017). ESM's
120 model residuals on NPP are calculated as the median of the difference between ESM's NPP and NPP from the global
inventory monitoring and modelling studies group (GIMMS). Lithology maps from the global lithological map (GLiM)
(Hartmann and Moosdorf, 2012) was used but since lithology was not significant ($p > 0.05$) and the model has a lower AIC



without it was not included in the final generalized additive mixed model presented here. All statistical analysis were made using R v3.5 (R Core Team, 2018).

125 3 Results

3.1 Global heterotrophic respiration flux and spatial biases

Global heterotrophic respiration flux simulated by the 13 ESMs ranges from 29 to 78 Pg C yr⁻¹ (Fig. 1), whereas the equivalent estimates for observationally derived products estimate range from 43 to 51 Pg C yr⁻¹. The multi-model mean of the ESMs (49 Pg C yr⁻¹) falls within the range of the observation-derived products. However, only four out of 13 ESMs
130 (BCC-CSM2-MR, CNRM-ESM2-1, IPSL-CM6A-LR, and SAM0-UNICOM) simulate an overall heterotrophic respiration flux that is within the range of the observation-derived products (Fig 1).

Despite similar global-scale values, regional-scale differences between the observation-derived products are much larger (Fig. 2). The Konings et al. (2019) product estimates large heterotrophic fluxes in the tropics and lower fluxes in other regions such as the west coast of Northern America or central Asia, as compared to the Warner et al. (2019) and the
135 Hashimoto et al. (2015) products that share similar spatial patterns. The mean of the 13 ESMs simulations also gives a much larger heterotrophic respiration fluxes over the tropics in particular over South-East Asia compared to any of the three observation-derived products. In general, the heterotrophic respiration fluxes from the 13 ESMs mean is closer to Konings et al. (2019) product over the tropics but closer to the Warner et al. (2019) and the Hashimoto et al., (2015) products over temperate regions. For boreal regions, the three observations-derived products and the 13 ESMs means are very close.

140 To generate our best-estimate of heterotrophic respiration fluxes from the three observation-derived products we calculated the median for each cell. We then compared each ESM with the observation-derived products median (Fig. 3). This comparison indicates that, apart from the ESM NorCPM1, ESMs tend to overestimate heterotrophic respiration flux in tropical regions (approx. 1,000 gC m⁻² yr⁻¹ for MPI-ESM1-2-LR over the Amazon or 1,500 gC m⁻² yr⁻¹ for UKESM1-0-LL over South-East Asia, for instance). Models perform relatively well in temperate regions with for instance bias close to 0 gC
145 m⁻² yr⁻¹ for BCC-ESM-1 over North America and Europe. Importantly, the four models that predict a global heterotrophic respiration flux within the range given by the observation-derived products (BCC-CSM2-MR, CNRM-ESM2-1, IPSL-CM6A-LR and SAM0-UNICOM), do not perform well at finer scales - with over estimation of the flux in some regions and under estimation in others. Therefore, this good global-scale performance masks spatial bias compensation.

3.2 Identification of the major drivers of the heterotrophic respiration bias in earth system models.



150 In order to improve predictions of heterotrophic respiration fluxes in future ESMs it is key that we understand the spatial
biases we observed and what their causes are. To explore these biases, we performed a statistical analysis based on a
generalized additive mixed model of the ESMs residuals defined as the median of the difference between each CMIP6's
model output and the median of the observation-based products calculated in each grid cell (see online methods). We
performed the residual analysis on the ESMs median rather on each individual model because the ESMs soil carbon module
155 share a very common approach based on first order kinetics with soil organic decomposition driven by soil moisture and
temperature (Ito et al., 2020). This approach is derived from the very first attempts to describe soil organic decomposition
with mathematical equations (Henin and Dupuis, 1945) and is still the most used to describe this process (Manzoni and
Porporato, 2009; Wutzler et al., 2008). Thus, performing analysis on the median instead of each single model can provide
broader suggestions to improve ESMs performances.

160 Since the drivers of heterotrophic respiration are soil carbon availability, soil moisture and temperature, carbon inputs and
mineralogy (Doetterl et al., 2015), we used soil organic carbon, net primary production residuals calculated using similar
methods to heterotrophic respiration flux residuals, mean annual precipitation, mean annual temperature and lithology as
explaining variables. Our method identified the main drivers of ESMs residuals as soil organic carbon, net primary
production residuals, mean annual precipitation, and mean annual temperature (Fig. 4). Lithology was not significant
165 ($p > 0.05$) and the model has a lower AIC without this variable and so we did not include lithology in the final model
presented here. We observed that the residuals due to soil organic carbon stock are close to zero for soil with a low carbon
stock but heterotrophic respiration is under estimated by ESMs for soils rich in organic carbon ($> 3,000 \text{ g C m}^{-2}$) (Fig. 4a).
The model residuals on the heterotrophic respiration flux are partially explained by the model residuals on net primary
production with a slight increase from model underestimation to model overestimation when model residual on net primary
170 production increase from $-1,000$ to $400 \text{ g C m}^{-2} \text{ yr}^{-1}$. We noted that when net primary production fits well with satellite
products (i.e. model residuals close to $0 \text{ g C m}^{-2} \text{ yr}^{-1}$), the ESM residuals on the heterotrophic respiration flux are also close to
 $0 \text{ g C m}^{-2} \text{ yr}^{-1}$. For a few grid cells where ESMs largely overestimate net primary production (i.e. model residuals higher than
 $400 \text{ g C m}^{-2} \text{ yr}^{-1}$), the ESMs residuals on heterotrophic respiration flux tend to be negative suggesting that ESM
underestimate heterotrophic respiration flux. The clearest tendency we obtained was with mean annual precipitation, the
175 more it increases the more the models overestimate the heterotrophic respiration flux (Fig. 4c). The median ESMs residual
was also partially controlled by mean annual temperature (Fig. 4d) with a relatively low overestimation by the models for
cold temperatures such as those recorded in polar climate zones and in some continental climate zones (e.g. subarctic
climate), a relatively good fit for temperature between 270 and 290K corresponding to temperate and some continental
climate zones (e.g. Hot summer continental climates) and then a sudden underestimation for warm temperatures above 290K
180 corresponding to tropical and dry climate zones.



4 Discussion

In this study we evaluated, for the first time, the ability of the ESMs to reproduce heterotrophic respiration flux. Indeed, so far heterotrophic respiration in ESMs could only by constraint indirectly by constraining net ecosystem exchange fluxes or through ecosystem respiration in which heterotrophic respiration is just one component among many others. We showed that only four of 13 of the CMIP models produce global-scale estimates that are consistent with observation-derived products. However, we also showed that this consistency was due to spatial bias compensations driven by different environmental variables. Heterotrophic respiration represents a carbon flux that is roughly five times that of anthropogenic emissions (Friedlingstein et al., 2020) and, as such, it is vital that work is done to improve the ability of ESMs to reproduce this flux. Nevertheless, we also observed large discrepancies between observation-based products showing that our ability to provide heterotrophic flux based on observations is not optimal. To better constrain ESMs projections, some efforts are needed to reduce uncertainties between observation-based products.

However, working only on heterotrophic respiration may not be sufficient to improve the entire soil organic carbon module of the ESMs. ESM capacities to reproduce observed soil organic carbon stocks also need to be improved (Ito et al., 2020; Varney et al., 2022). To improve both soil organic carbon stocks and heterotrophic respiration fluxes soil organic carbon decomposition rates needs to be better constrained. The ESM residual analysis we performed here suggests some new research avenues and in particular for the response of the major drivers. First, it must be noted that most of the boundary conditions of the soil organic carbon modules of an ESM are calculated by the ESM itself. Thus, if soil moisture, soil temperature or litter production are incorrect, the soil organic carbon dynamic cannot be correct. We observed that when the residual of NPP was close to zero the residual on heterotrophic respiration is also close to zero. Thus, improving the plant functioning scheme may ultimately improve the capacities of the ESMs to reproduce the heterotrophic respiration flux. Our study also showed that mean annual temperature is an important driver of the ESM residuals in particular for hot regions with large underestimations of the flux. It probably corresponds to very arid regions since for most of the ESMs, heterotrophic respiration fluxes from regions like Australia, Middle East or Northern Africa tend to be underestimated. The response of soil organic decomposition by microorganisms is likely to be temperature dependent, with lower rates of decomposition seen in cold regions and higher rates in hot regions (Wang et al., 2010; Zhou et al., 2009). In contrast, the response of soil organic decomposition to temperature in ESMs is generally controlled by Q10 equations (Davidson and Janssens, 2006) with fixed parameters not dynamic and not spatially distributed (Ito et al., 2020). Having more flexible Q10 parameters may help to improve ESMs capacities to reproduce observation-derived products of heterotrophic respiration fluxes. Moreover, land surface scheme of ESMs are known to be very sensitive to Q10 values (Jones et al., 2003).

Finally, we observed a relatively linear, positive relationship between mean annual precipitation and the ESMs' residuals. This response is probably driven by soil moisture because it is a key driver of microbial activity and therefore of heterotrophic respiration fluxes (Moyano et al., 2012). ESMs use three main groups of soil moisture response function



(Falloon et al., 2011): i) some models do not represent soil moisture effect, ii) some models increase soil organic decomposition when soil moisture increases assuming less water limitation for microbial activity and iii) some models
215 assume a humped relationship between soil moisture and soil organic decomposition, with high decomposition at intermediate soil moisture and low decomposition in very wet soils where microbial activity is reduced because of limitation by oxygen availability and in dry soils where microbial activity is reduced because of limitation by water. As with Q10, the land surface schemes are highly sensitive to the soil moisture response function chosen approach and most of the ESMs use option ii) (Varney et al., 2022). Soil incubations have repeatedly shown that the response of heterotrophic respiration fluxes
220 to soil moisture is approximated by a bell-shaped function with parameters depending on soil organic carbon, soil clay content, and soil bulk density (Moyano et al., 2012). Thus, for wet soils, heterotrophic respiration fluxes are probably reduced because of oxygen limitation. Implementing this bell-shaped function approach is necessary to accurately represent the soil organic carbon stock of peatland in some land surface schemes used by ESMs (Qiu et al., 2019). Not considering the possible oxygen limitation effect on wet soils can explain why ESMs tends to overestimate the heterotrophic respiration flux
225 when mean annual precipitation is high. Changing soil moisture function to better represent this effect should be relatively easy and may substantially improve the capacities of ESMs to reproduce the heterotrophic respiration flux.

Another important parameter controlling heterotrophic respiration flux is carbon use efficiency defined as the ratio between the carbon remaining in a system and the carbon entering that system (Manzoni et al., 2018). In our context this is the ratio between the carbon mineralized through microbial heterotrophic respiration and the carbon incorporated into the microbial
230 biomass. The heterotrophic respiration flux therefore results from two processes in ESMs, the soil organic carbon decomposition and its allocation to other soil carbon pools or to heterotrophic respiration. Carbon use efficiency is highly variable and depends on several biotic and abiotic factors (Manzoni, 2017; Manzoni et al., 2012; Sinsabaugh et al., 2013). In ESMs, carbon use efficiency is not dynamic and not spatially distributed, thus having flexible carbon use efficiency control may help to reproduce observations (Zhang et al., 2018). A simple approach that may aid a better representation of
235 heterotrophic respiration fluxes is optimizing the carbon use efficiency parameters of the ESMs using a Bayesian approach as is done for other land fluxes (Kuppel et al., 2012). This would result in a spatially distributed set of parameters for carbon use efficiency but this approach would not be dynamic. Another option might to benefit to the current large carbon use efficiency measures existing in the literature (Manzoni et al., 2012) to define statistical functions predicting carbon use efficiency based on explanatory variables that could themselves be dynamic (soil temperature, pH, soil C:N ratio, etc.). Thus,
240 carbon use efficiency might be spatialized and dynamic.

A better representation of the heterotrophic respiration flux is also important for other biogeochemical variables in particular in ESMs with explicit nitrogen cycle representation in their land surface scheme. Indeed, heterotrophic respiration fluxes are indicators of soil organic carbon decomposition but when nitrogen is explicitly represented it also becomes an indicator of soil N mineralization (Vuichard et al., 2018). In the field, the soil organic matter is composed by complex molecules made of
245 carbon and nitrogen among others (Cleveland and Liptzin, 2007). Microorganisms decompose soil organic matter releasing



CO₂ to the atmosphere and mineral nitrogen to the soil solution. Microbial activity is therefore a major driver of mineral nitrogen availability and partially control nitrogen limitation on primary production and therefore on land carbon sink (Bragazza et al., 2013). Since more and more ESM represent explicitly the nitrogen cycle in their land surface scheme (Davies-Barnard et al., 2020; Varney et al., 2022) constraining well the heterotrophic respiration flux may help to constrain the nitrogen mineralization flux as they both come from the soil organic matter decomposition by extracellular enzymes. A better representation of the mineral N release flux would probably, in turn, improve the simulation of NPP.

5 Conclusion

Our study showed that despite the absence of constraint on the heterotrophic respiration flux before the CMIP6 exercise, a few current ESMs are fairly representing the total heterotrophic respiration flux but all failed at representing the spatial distribution. Since heterotrophic fluxes are large and are a major determinant of whether land surfaces represent a carbon sink or source it is of major importance to better constrain these fluxes and how they will be impacted by climate and land use changes. We showed that current ESMs failed to reproduce heterotrophic respiration fluxes where precipitation is important probably because heterotrophic respiration responses to soil moisture are poor representations of reality. Nevertheless, it is important to note that soil moisture is not only driven by precipitation. Other water fluxes like runoff, drainage and evapotranspiration affect the water balance in soils. In this study we did not directly consider soil moisture because it was not available for all the ESMs. Another limitation of our study is that we did not account for other important drivers of heterotrophic respiration in our model residual analysis like pH, microbial biomass, nitrogen availability, etc. We decided to focus on explanatory variables calculated by all the models because we aimed to identify biases due to feedbacks between ESMs variables rather than identifying missing mechanisms. We propose several options to improve the ESM without deep modifications of the current schemes. Our propositions might be easily implemented in the next ESMs generation resulting in possible substantial improvements.

Data availability

All data are available in the main text.

Author contributions

BG, LC, PB and LB designed the study, BG, JO, OT and LS performed the analysis. All the authors participated to the results interpretation and to the writing.

Competing interests

All other authors declare they have no competing interests.



Acknowledgments

280 The IPSL-CM6 experiments were performed using the HPC resources of TGCC under the allocations 2019-A0060107732, 2020-A0080107732 and 2021-A0100107732 (project gencmip6) provided by GENCI (Grand Equipement National de Calcul Intensif). The IPSL-CM6 team of the IPSL Climate Modelling Centre (<https://cmc.ipsl.fr>) is acknowledged for having developed, tested, evaluated, tuned the IPSL climate model, as well as performed and published the CMIP6 experiments. This study benefited from the ESPRI computing and data centre (<https://mesocentre.ipsl.fr>) which is supported by CNRS, 285 Sorbonne Université, Ecole Polytechnique and CNES as well as through national and international grants. BG acknowledges the Climat AmSud program grant REPRISE 21-CLIMAT-13 for funding.

References

- Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data., *Biogeosciences* [online] Available from: <http://biogeosciences.net/7/1915/2010/bg-7-1915-2010.pdf> (Accessed 20 May 2014), 2010.
- 290 Bond-Lamberty, B., Wang, C. and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, *Glob. Chang. Biol.*, 10(10), 1756–1766, doi:10.1111/j.1365-2486.2004.00816.x, 2004.
- Bragazza, L., Parisod, J., Buttler, A. and Bardgett, R. D.: Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands, *Nat. Clim. Chang.*, 3(3), 273–277, doi:10.1038/nclimate1781, 2013.
- Chabbi, A., Lehmann, J., Ciais, P., Loescher, H. W., Cotrufo, M. F., Don, A., SanClements, M., Schipper, L., Six, J., Smith, 295 P. and Rumpel, C.: Aligning agriculture and climate policy, *Nat. Clim. Chang.*, 7(5), 307–309, doi:10.1038/nclimate3286, 2017.
- Ciais, P., Yao, Y., Gasser, T., Baccini, A., Wang, Y., Lauerwald, R., Peng, S., Bastos, A., Li, W., Raymond, P. A., Canadell, J. G., Peters, G. P., Andres, R. J., Chang, J., Yue, C., Dolman, A. J., Haverd, V., Hartmann, J., Laruelle, G., Konings, A. G., King, A. W., Liu, Y., Luyssaert, S., Maignan, F., Patra, P. K., Peregon, A., Regnier, P., Pongratz, J., Poulter, B., Shvidenko, 300 A., Valentini, R., Wang, R., Broquet, G., Yin, Y., Zscheischler, J., Guenet, B., Goll, D. S., Ballantyne, A.-P., Yang, H., Qiu, C. and Zhu, D.: Empirical estimates of regional carbon budgets imply reduced global soil heterotrophic respiration, *Natl. Sci. Rev.*, 2(February), doi:10.1093/nsr/nwaa145, 2021.
- Cleveland, C. C. and Liptzin, D.: C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass, *Biogeochemistry*, 85(3), 235–252 [online] Available from: <http://www.springerlink.com/index/405P1URP48022221.pdf>, 305 2007.
- Davidson, E. a and Janssens, I. a: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change., *Nature*, 440(7081), 165–73, doi:10.1038/nature04514, 2006.
- Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., Fisher, R. A., Jones, C. D., Lee, H., Peano, D., Smith, B., Wärlind, D., Wiltshire, A. J., Wärlind, D., Wiltshire, A. J., Wärlind, D. and Wiltshire, A. J.: Nitrogen



- 310 cycling in CMIP6 land surface models: Progress and limitations, *Biogeosciences*, 17(20), 5129–5148, doi:10.5194/bg-17-5129-2020, 2020.
- Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E. and Boeckx, P.: Soil carbon storage controlled by interactions between geochemistry and climate, *Nat. Geosci.*, (September), doi:10.1038/ngeo2516, 2015.
- 315 Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J. and Taylor, K. E.: Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization, *Geosci. Model Dev.*, 9(5), 1937–1958, doi:10.5194/gmd-9-1937-2016, 2016.
- Falloon, P., Jones, C. D., Ades, M. and Paul, K.: Direct soil moisture controls of future global soil carbon changes: An important source of uncertainty, *Global Biogeochem. Cycles*, 25(3), 1–14, doi:10.1029/2010GB003938, 2011.
- 320 Friedlingstein, P., O’Sullivan, M., Jones, M. W., Andrew, R. M., Hauck, J., Olsen, A., Peters, G. P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S., Aragão, L. E. O. C. O. C., Arneeth, A., Arora, V., Bates, N. R., Becker, M., Benoit-Cattin, A., Bittig, H. C., Bopp, L., Bultan, S., Chandra, N., Chevallier, F., Chini, L. P., Evans, W., Florentie, L., Forster, P. M., Gasser, T., Gehlen, M., Gilfillan, D., Gkritzalis, T., Gregor, L., Gruber, N., Harris, I., Hartung, K., Haverd, V., Houghton, R. A., Ilyina, T., Jain, A. K., Joetzjer, E., Kadono, K., Kato, E., Kitidis, V.,
- 325 Korsbakken, J. I., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Liu, Z., Lombardozi, D., Marland, G., Metzl, N., Munro, D. R., Nabel, J. E. M. S. M. S., Nakaoka, S. I., Niwa, Y., O’Brien, K., Ono, T., Palmer, P. I., Pierrot, D., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Smith, A. J. P. P., Sutton, A. J., Tanhua, T., Tans, P. P., Tian, H., Tilbrook, B., Van Der Werf, G., Vuichard, N., Walker, A. P., Wanninkhof, R., Watson, A. J., Willis, D., Wiltshire, A. J., Yuan, W., Yue, X. and Zaehle, S.: Global Carbon Budget 2020, *Earth Syst. Sci. Data*, 12(4),
- 330 3269–3340, doi:10.5194/essd-12-3269-2020, 2020.
- Hartmann, J. and Moosdorf, N.: The new global lithological map database GLiM: A representation of rock properties at the Earth surface, *Geochemistry, Geophys. Geosystems*, 13(12), 1–37, doi:10.1029/2012GC004370, 2012.
- Hashimoto, S., Carvalhais, N., Ito, A., Migliavacca, M., Nishina, K. and Reichstein, M.: Global spatiotemporal distribution of soil respiration modeled using a global database, *Biogeosciences*, 12(13), 4121–4132, doi:10.5194/bg-12-4121-2015,
- 335 2015.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangquan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S. and Kempen, B.: SoilGrids250m: Global gridded soil information based on machine learning., 2017.
- 340 Henin, S. and Dupuis, M.: Essai de bilan de la matière organique du sol, *Ann. d’Agronomie*, 1, 6–27, 1945.
- Ito, A., Hajima, T., Lawrence, D. M., Brovkin, V., Delire, C., Guenet, B., Jones, C. D., Malyshev, S., Materia, S., McDermid, S. P., Peano, D., Pongratz, J., Robertson, E., Shevliakova, E., Vuichard, N., Wårlind, D., Wiltshire, A. and Ziehn, T.: Soil carbon sequestration simulated in CMIP6-LUMIP models: Implications for climatic mitigation, *Environ. Res.*



- Lett., 15(12), 124061, doi:10.1088/1748-9326/abc912, 2020.
- 345 Jones, C. D. D., Cox, P. and Huntingford, C.: Uncertainty in climate–carbon-cycle projections associated with the sensitivity of soil respiration to temperature, *Tellus B*, 55(2), 642–648 [online] Available from: <http://onlinelibrary.wiley.com/doi/10.1034/j.1600-0889.2003.01440.x/full> (Accessed 21 January 2011), 2003.
- Konings, A. G., Anthony Bloom, A., Liu, J., Parazoo, N. C., Schimel, D. S. and Bowman, K. W.: Global satellite-driven estimates of heterotrophic respiration, *Biogeosciences*, 16(11), 2269–2284, doi:10.5194/bg-16-2269-2019, 2019.
- 350 Kuppel, S., Peylin, P., Chevallier, F., Bacour, C., Maignan, F. and Richardson, a. D.: Constraining a global ecosystem model with multi-site eddy-covariance data, *Biogeosciences*, 9(10), 3757–3776, doi:10.5194/bg-9-3757-2012, 2012.
- Luyssaert, S., Marie, G., Valade, A., Chen, Y., Njakou Djomo, S., Ryder, J., Otto, J., Naudts, K., Lansø, A. S., Ghattas, J. and McGrath, M. J.: Trade-offs in using European forests to meet climate objectives, *Nature*, 562(7726), 259–262, doi:10.1038/s41586-018-0577-1, 2018.
- 355 Manzoni, S.: Flexible carbon-use efficiency across litter types and during decomposition partly compensates nutrient imbalances-results from analytical stoichiometric models, *Front. Microbiol.*, 8(APR), 1–15, doi:10.3389/fmicb.2017.00661, 2017.
- Manzoni, S. and Porporato, A.: Soil carbon and nitrogen mineralization: Theory and models across scales, *Soil Biol. Biochem.*, 41(7), 1355–1379, doi:10.1016/j.soilbio.2009.02.031, 2009.
- 360 Manzoni, S., Taylor, P., Richter, A., Porporato, A. and Ågren, G. I.: Environmental and stoichiometric controls on microbial carbon-use efficiency in soils, *New Phytol.*, 196(1), 79–91, doi:10.1111/j.1469-8137.2012.04225.x, 2012.
- Manzoni, S., Capek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Vico, G., Way, D., Čapek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Brüchert, V., Frouz, J., Herrmann, A. M., Lindahl, B. D., Lyon, S. W., Šantrůčková, H., Vico, G., Way, D., Capek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Vico, G., Way, D., Čapek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Brüchert, V., Frouz, J., Herrmann, A. M., Lindahl, B. D., Lyon, S. W., Šantrůčková, H., Vico, G., Way, D., Capek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Vico, G. and Way, D.: Reviews and syntheses: Carbon use efficiency from organisms to ecosystems – definitions, theories, and empirical evidence, *Biogeosciences*, 15, 5929–5949, doi:10.5194/bg-2018-275, 2018.
- Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gommis, M. I. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R. B. R., Maycock, T. K. K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gommis, M. I. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R. B. R., Maycock, T. K. K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gommis, M. I. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R. B. R., Maycock, T. K. K., Waterfield, T., Yelekçi, O., Yu, R. and Zhou, B.: Climate change 2021: The physical science basis summary for policymakers. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press., 2021.
- 375 Moyano, F. E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Curiel Yuste, J., Don, a., Epron, D., Formanek, P.,



- Franzluebbers, a., Ilstedt, U., Kätterer, T., Orchard, V., Reichstein, M., Rey, a., Ruamps, L., Subke, J. -a., Thomsen, I. K. and Chenu, C.: The moisture response of soil heterotrophic respiration: interaction with soil properties, *Biogeosciences*, 9(3), 1173–1182, doi:10.5194/bg-9-1173-2012, 2012.
- 380 Qiu, C., Zhu, D., Ciais, P., Guenet, B., Peng, S., Krinner, G., Tootchi, A., Ducharne, A. and Hastie, A.: Modelling northern peatlands area and carbon dynamics since the Holocene with the ORCHIDEE-PEAT land surface model (SVN r5488), *Geosci. Model Dev.*, 12, 2961–2982, doi:10.5194/gmd-2018-256, 2019.
- Raich, J. W. W., Potter, C. S. S. and Bhagawati, D.: Interannual variability in global soil respiration, 1980–94, *Glob. Chang. Biol.*, 8(8), 800–812, doi:10.1046/j.1365-2486.2002.00511.x, 2002.
- 385 Scharlemann, J. P., Tanner, E. V., Hiederer, R. and Kapos, V.: Global soil carbon: understanding and managing the largest terrestrial carbon pool, *Carbon Manag.*, 5(1), 81–91, doi:10.4155/cmt.13.77, 2014.
- Séférian, R., Berthet, S., Yool, A., Palmiéri, J., Bopp, L., Tagliabue, A., Kwiatkowski, L., Aumont, O., Christian, J., Dunne, J., Gehlen, M., Ilyina, T., John, J. G., Li, H., Long, M. C., Luo, J. Y., Nakano, H., Romanou, A., Schwinger, J., Stock, C., 390 Santana-Falcón, Y., Takano, Y., Tjiputra, J., Tsujino, H., Watanabe, M., Wu, T., Wu, F. and Yamamoto, A.: Tracking Improvement in Simulated Marine Biogeochemistry Between CMIP5 and CMIP6, *Curr. Clim. Chang. Reports*, 6(3), 95–119, doi:10.1007/s40641-020-00160-0, 2020.
- Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L. and Richter, A.: Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling., *Ecol. Lett.*, 16(7), 930–939, doi:10.1111/ele.12113, 2013.
- 395 Subke, J. A., Inglisma, I. and Cotrufo, M. F.: Trends and methodological impacts in soil CO₂ efflux partitioning: A metaanalytical review, *Glob. Chang. Biol.*, 12(6), 921–943, doi:10.1111/j.1365-2486.2006.01117.x, 2006.
- Varney, R. M., Chadburn, S. E., Burke, E. J. and Cox, P. M.: Evaluation of soil carbon simulation in CMIP6 Earth System Models, *Biogeosciences*, 6(January), 4671–4704, 2022.
- Vuichard, N., Messina, P., Luyssaert, S., Guenet, B., Zaehle, S., Ghattas, J., Bastrikov, V. and Peylin, P.: Accounting for 400 Carbon and Nitrogen interactions in the Global Terrestrial Ecosystem Model ORCHIDEE (trunk version, rev 4999): multi-scale evaluation of gross primary production, *Geosci. Model Dev.*, 12(November 2018), 1–41, doi:10.5194/gmd-2018-261, 2018.
- Wang, X., Piao, S., Ciais, P., Janssens, I. a., Reichstein, M., Peng, S. and Wang, T.: Are ecological gradients in seasonal Q₁₀ of soil respiration explained by climate or by vegetation seasonality?, *Soil Biol. Biochem.*, 42(10), 1728–1734, 405 doi:10.1016/j.soilbio.2010.06.008, 2010.
- Warner, D. L., Bond-Lamberty, B., Jian, J., Stell, E. and Vargas, R.: Spatial Predictions and Associated Uncertainty of Annual Soil Respiration at the Global Scale, *Global Biogeochem. Cycles*, 33(12), 1733–1745, doi:10.1029/2019GB006264, 2019.
- Wutzler, T., Reichstein, M. and Discussions, B.: Colimitation of decomposition by substrate and decomposers- a comparison 410 of model formulations, *Biogeosciences*, 5(3), 749–759, doi:10.5194/bg-5-749-2008, 2008.
- Zhang, H., Goll, D. S., Manzoni, S., Ciais, P., Guenet, B. and Huang, Y.: Modeling the effects of litter stoichiometry and soil



mineral N availability on soil organic matter formation using CENTURY-CUE (v1.0), *Geosci. Model Dev.*, 11(12), 4779–4796, doi:10.5194/gmd-11-4779-2018, 2018.

415 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 Sens. Environ.*, 95(2), 164–176, doi:10.1016/j.rse.2004.12.011, 2005.

Zhou, T., Shi, P., Hui, D. and Luo, Y.: Global pattern of temperature sensitivity of soil heterotrophic respiration (Q_{10}) and its implications for carbon-climate feedback, *J. Geophys. Res.*, 114(G2), G02016, doi:10.1029/2008JG000850, 2009.



420 Figures

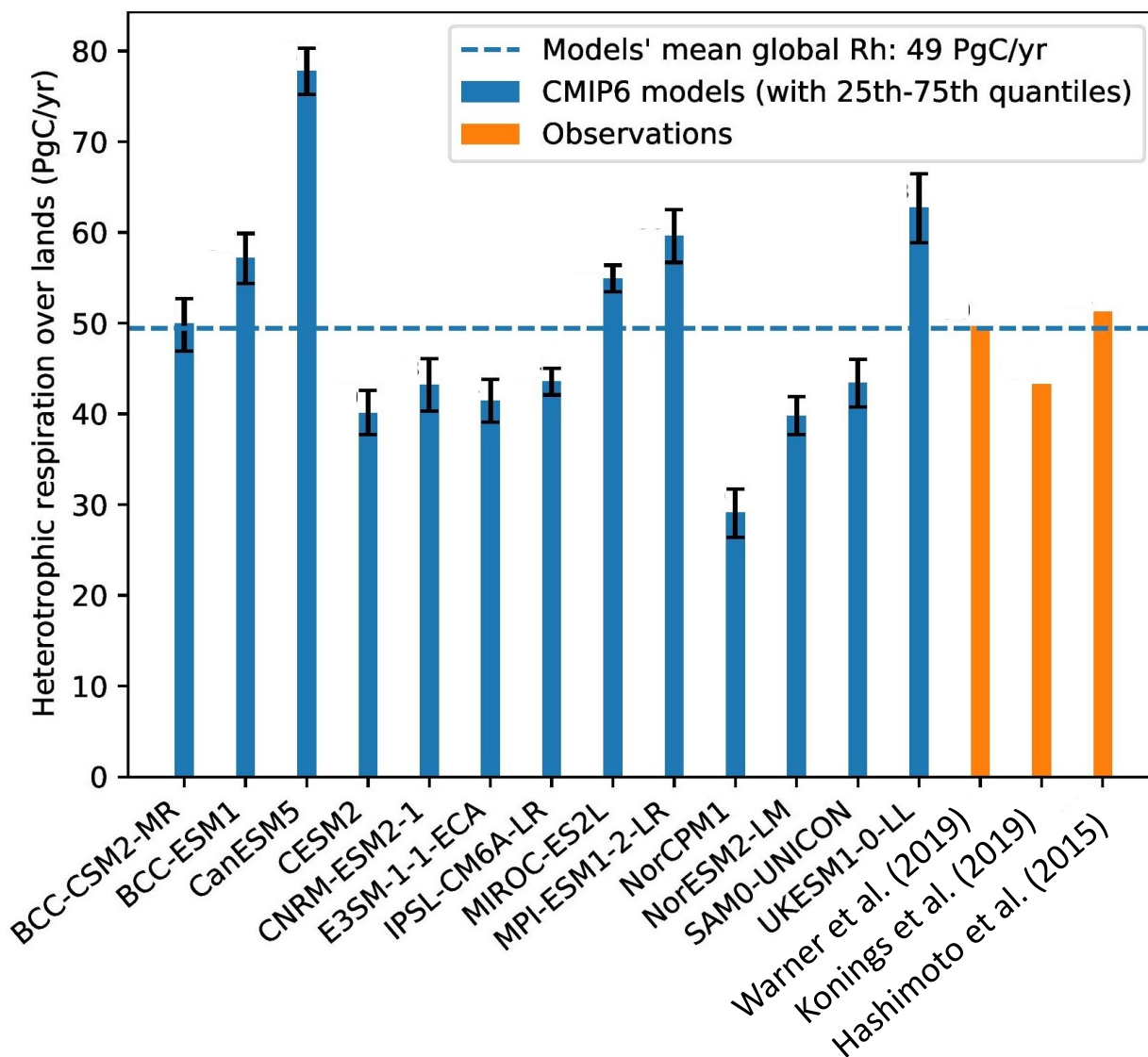
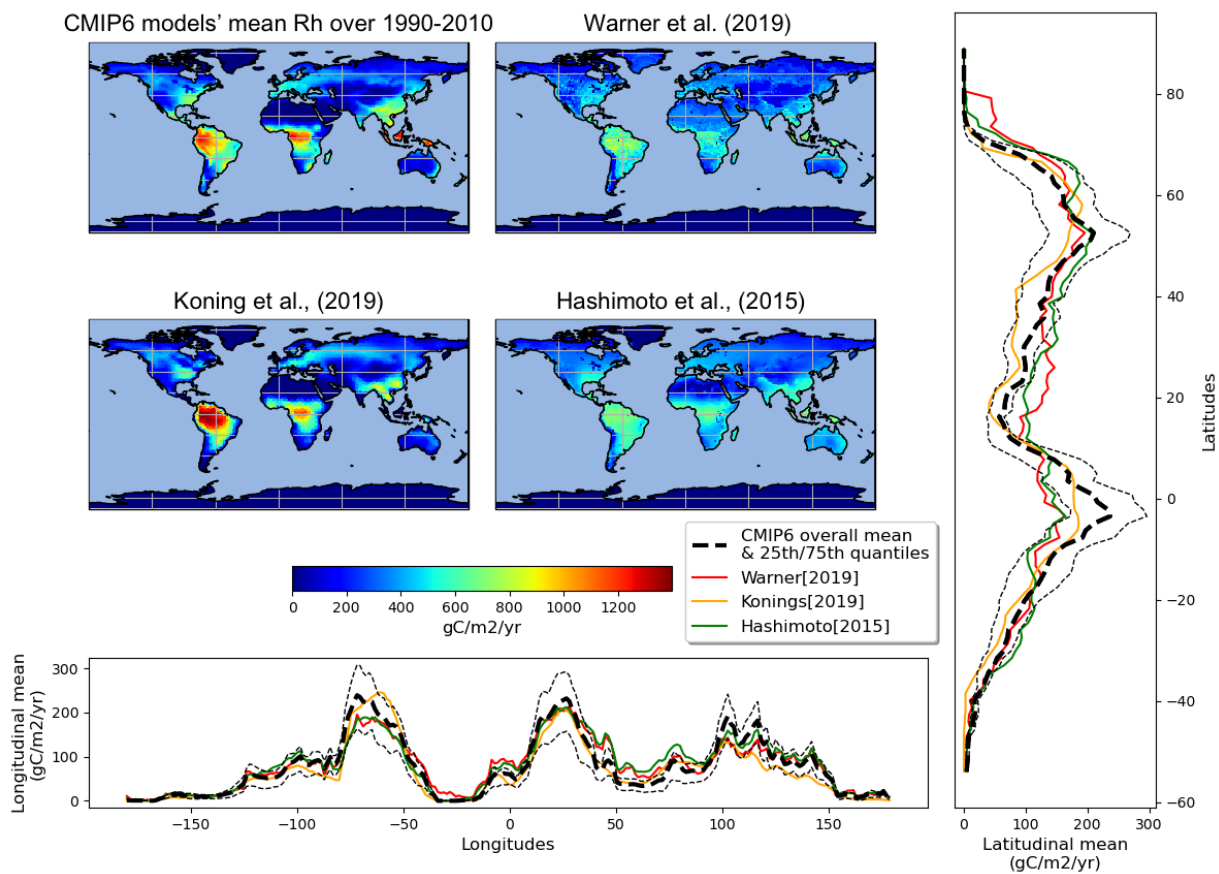


Fig. 1. Global estimations of soil heterotrophic respiration mean over 1990-2010 period.



425

Fig. 2. Comparison of mean soil heterotrophic respiration spatial distribution among mean CMIP6 outputs and observation data.

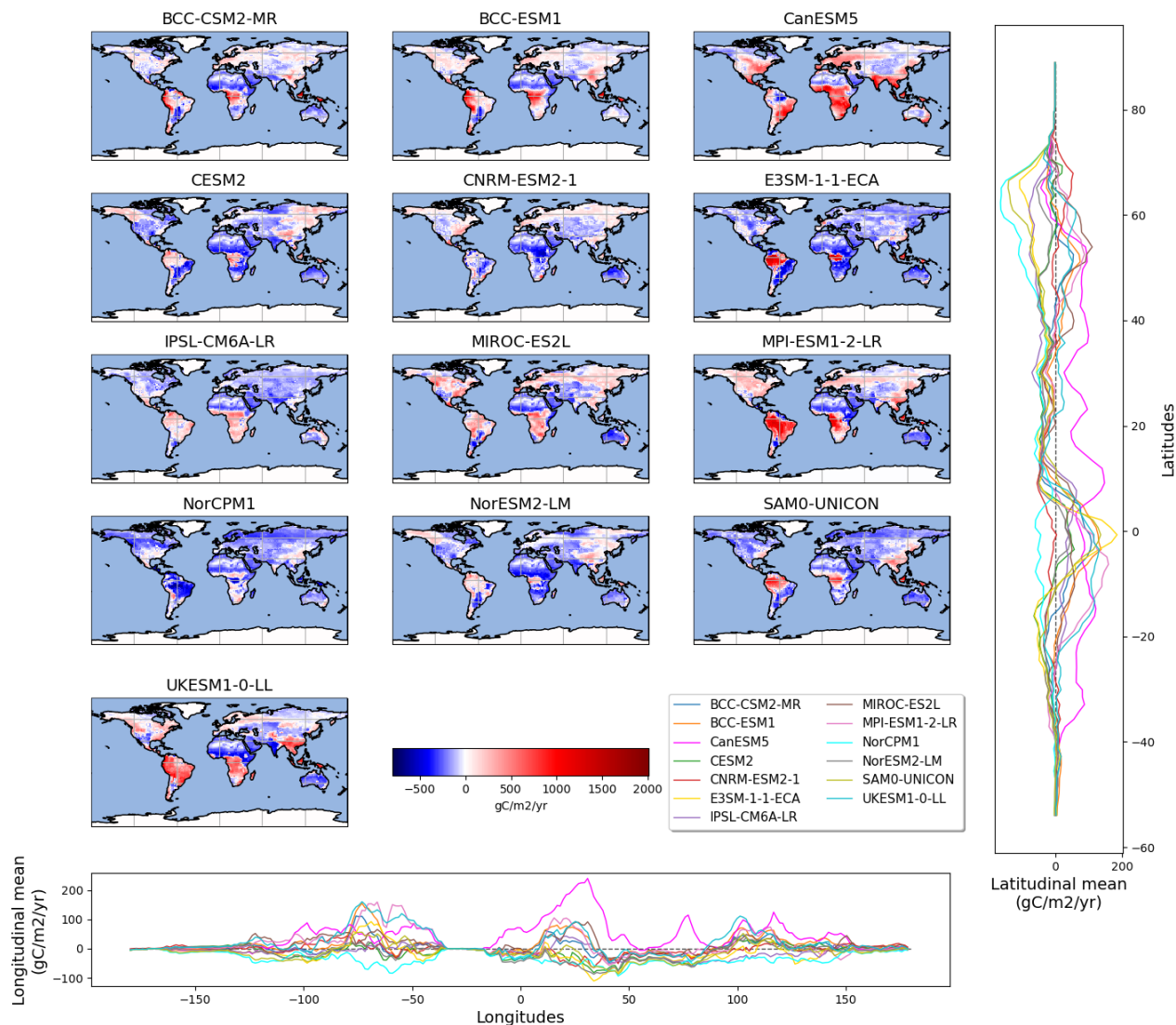


Fig. 3. Spatially distributed residuals of CMIP6 ESMs predictions over the period 1990-2010 with respect to median observation products.

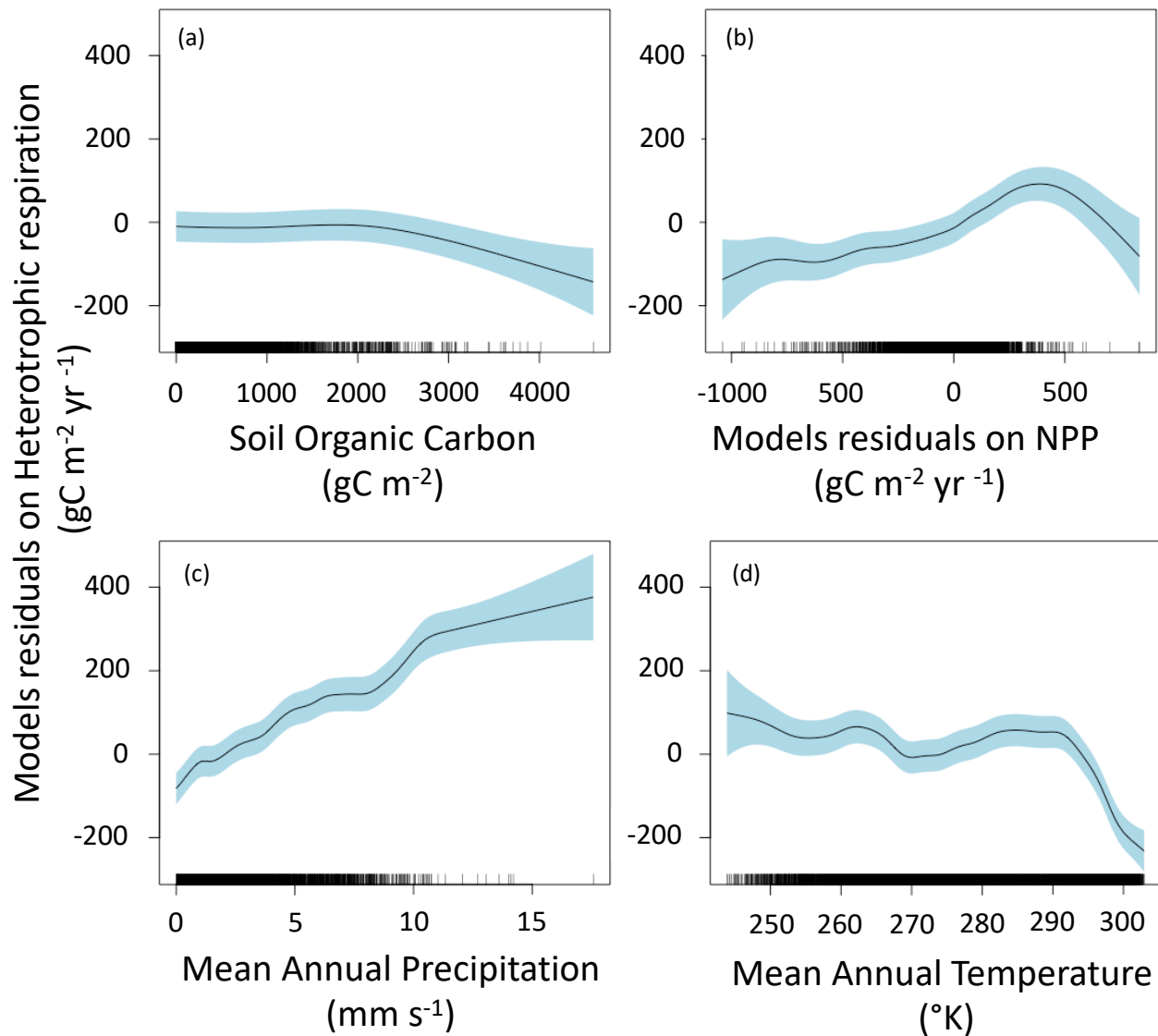


Fig. 4. Median of ESMs residuals on soil heterotrophic respiration. The residuals are explained by soil organic carbon (a), median of NPP residuals (b), mean annual precipitation (c) and mean annual temperature (d). Negative values mean model underestimation.