Vertically Divergent Responses of SOC Decomposition to Soil Moisture in a Changing Climate

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Abstract The role of soil moisture for organic matter decomposition rates remains poorly understood and underrepresented in Earth System Models (ESMs). We apply the Dual Arrhenius Michaelis-Menten (DAMM) model to a selection of ESM soil temperature and moisture outputs to investigate their effects on decomposition rates, at different soil depths, for a historical period and a future climate period. Our key finding is that the inclusion of soil moisture controls has diverging effects on both the speed and direction of projected decomposition rates (up to ±20%), compared to a temperature-only approach. In the top soil, the majority of these changes is driven by substrate availability. In deeper soil layers, oxygen availability plays a relatively stronger role. Owing to these different moisture controls along the soil depth, our study highlights the need for depth-resolved inclusion of soil moisture effects on decomposition rates within ESMs. This is particularly important for C-rich soils in regions which may be subject to strong future warming and vertically opposing moisture changes, such as the peat soils at northern high latitudes.

Plain Language Summary Soils contain a lot of carbon (C). Earth System Models (ESMs) predict that the amount of C released from soils into the atmosphere as CO_2 will increase in response to increased warming and microbial activity. Soil moisture also controls microbial C decomposition, but most ESMs do not yet describe this process very well. In this study we apply a simple equation to different ESMs, to see how both temperature and soil moisture change microbial decomposition under future climate. First, we show that the speed of C released into the atmosphere changes when we include soil moisture changes, compared to what is expected due to warming alone. Second, we found that the future speed at which carbon that can be decomposed in the topsoil mainly depends on how much carbon microbes have access to, but that in the deeper soil this process becomes much more affected by the absence/presence of oxygen. Including these soil moisture interactions in ESMs for different soil depths is important to predict whether soils will store more or less C in the future. Our findings are particularly relevant for high latitude soils which store large amounts of C, will warm fast, and experience frequent (re)wetting and drying.

1. Introduction

Soil organic carbon (SOC) is the largest terrestrial carbon pool, but it is still uncertain how it will respond to climate change in the 21st century (Bradford et al., 2016; Crowther et al., 2016; Gestel et al., 2018). Coupled climate modeling is a valuable tool to study climate–soil-carbon feedbacks, but there are large differences between existing model projections (e.g., Jones et al., 2013; Luo et al., 2016; Todd-Brown et al., 2013, 2014). This broad uncertainty partly reflects our lack of understanding and representation of the underlying processes (Sulman et al., 2018).

During the last decade, there has been a substantial shift in our perspective on the processes that determine the residence time of SOC in soils (Blankinship et al., 2018; Schmidt et al., 2011; Shi et al., 2020). Organic matter turnover is affected by several co-dependent factors and soil internal feedbacks (Davidson & Janssens, 2006; Heimann & Reichstein, 2008; Kirschbaum, 2006), such as temperature, soil moisture, oxygen availability, substrate availability and quality, stabilization of organic material by organo-mineral associations, and pH, with microbes as the main actors. This co-dependence of drivers of organic matter turnover can lead to non-linear system responses under future climate, a behavior which, due to their linear, first-order kinetics structure, conventional soil carbon decomposition models may not be able to capture (Falloon et al., 2011; Sierra et al., 2015; Wieder

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et al., 2018; Zhou et al., 2008). Yet, while these models do not reflect the latest scientific insights, they are actively used as coupled components within fully interacting ESMs.

The majority of coupled climate models currently in use include a soil component that uses a first-order decomposition rate for one or multiple carbon pools, generally sharing a similar mathematical structure (Sierra et al., 2012). The use of kinetic constants and response functions implicitly represents microbial interactions and nutrient dynamics (Schimel, 2001). Of particular importance are the dependencies of the decomposition rates on soil temperature and moisture, which, together with the biochemical recalcitrance of organic matter (and not explicit microbial interactions), determine the turnover rate of each carbon pool (Bradford & Fierer, 2012; Schimel, 2001; Schmidt et al., 2011; Todd-Brown et al., 2013). The temperature response functions generally prescribe faster decomposition at higher temperatures (Lloyd & Taylor, 1994; Sierra et al., 2015; Todd-Brown et al., 2018). However, the models' responses to moisture are less uniformly described: It is either not at all included, or only empirically described (Falloon et al., 2011; Sierra et al., 2015). Furthermore, classic soil carbon decomposition models typically do not consider soil temperature and moisture interactions over a vertically resolved SOC profile, and as a result fail to capture observed climate sensitivities of soil carbon turnover times (Ahrens et al., 2015; Braakhekke et al., 2011; Koven et al., 2013, 2017). Even recent microbially explicit models (e.g., CORPSE by Sulman et al., 2014, MIMICS by Wieder et al., 2014, DAMM-MCNIP by Abramoff et al., 2017) typically only consider one soil depth, even though many soil properties change with depth.

Data-driven studies clearly indicate that the feedback between climate and carbon turnover times strongly depends on temperature and the hydrological cycle on an ecosystem scale (Carvalhais et al., 2014; Jung et al., 2017; J. Wang et al., 2018). Locally, soil temperature and soil moisture are the two most important controlling factors of heterotropic respiration rates, and thereby the carbon turnover rate of soils (Davidson & Janssens, 2006; Moyano et al., 2013; Yan et al., 2018). For temperature, it is generally accepted that the rate of decomposition increases as temperature increases, until a certain maximum where enzymes start to break down (Hochachka & Somero, 2002; Nottingham et al., 2016). For soil moisture, there is more uncertainty in both the functional shape and the extremes of the response curves (Sierra et al., 2017), that is, how decomposition rates are affected by very dry or very wet soil moisture conditions and the shape of the response during drying/(re)wetting events. Decomposition rates can reach a potential maximum at optimal soil moisture (Figure S1 in Supporting Information S1): At this point, both the availability of decomposable substrates (organic matter) and oxygen (as an electron acceptor) are optimal (Moyano et al., 2013; Sierra et al., 2015; Skopp et al., 1990). As a soil dries out, its structure and hydraulic conductivity changes so that microbes will reduce their activity or even die under extremely low water potentials (Manzoni & Katul, 2014; Schimel, 2018). As a soil becomes wetter, oxygen availability for aerobic decomposition becomes scarcer, slowing down decomposition.

At this moment, encouraging new SOC decomposition modelling developments are made: For example, Wieder et al. (2019) list several examples, and see Wutzler et al. (2017); Yu et al. (2020). These advances have not yet found their way into the coupled global climate models used in the Coupled Model Inter-comparison Project (CMIP) ensembles, nor do they explicitly deal with improving the soil moisture responses. Here we propose another method to gain insight into the potential effects of soil temperature and moisture changes on future SOC decomposition rates among a vertical soil profile using a simple, semi-mechanistic modelling approach. Davidson et al. (2012) provide such a framework, called the Dual Arrhenius Michalis-Menten (DAMM) model. The process-based and empirically tested DAMM model consists of a set of three linked equations. The first term is an Arrhenius function to calculate a temperature dependent maximum decomposition rate (V_{max}). V_{max} is multiplied with two moisture dependent Michaelis-Menten terms (MM-terms). Without explicitly simulating microbial biomass, the MM-terms describe the necessary diffusion of substrate and oxygen towards the microbial surface for decomposition. If substrate or oxygen availability are limiting, the decomposition rate is reduced.

Our goal is to quantify how under a changing climate, decomposition rates change in response to soil moisture changes, separate from the temperature-driven changes, as well as their combined effects. In addition, we investigate the effect of soil moisture along a vertical gradient and the implications for predicted decomposition rates. We run the DAMM model with vertically explicit SOC data, and vertically resolved CMIP5 model outputs for soil moisture and soil temperature. We calculate the temperature- and soil moisture driven decomposition rate changes between a historic (1976–2005) simulation period and a future climate change period (2070–2099), following Representative Concentration Pathway 8.5 (RCP8.5). This generates global maps that outline the various temperature and soil moisture driven effects on decomposition rates at different depths. Our study highlights the

possible magnitude of decomposition rate changes with projected soil moisture (and temperature) changes, in conjunction with spatially varying SOC content at different soil depths.

2. Data and Methods

2.1. The DAMM Model

The DAMM model by Davidson et al. (2012) uses a set of linked equations to study the simultaneous effects of soil temperature and soil moisture on organic matter decomposition. The DAMM models' functions are based on process concepts, and successfully developed and repeatedly tested using empirical data (Abramoff et al., 2017; Davidson et al., 2012; Drake et al., 2018; Sihi et al., 2018). We briefly summarize these equations here, but for full methods and references redirect the reader to the original paper. The DAMM model calculates the decomposition rate R_{Sx} of a substrate (S_x):

$$R_{Sx} = V_{max} \cdot MM_{Sx} \cdot MM_{O2} \tag{1}$$

V_{max} is an Arrhenius function for the maximum reaction velocity of R_{Sx}, and two reverse MM-terms represent the reduction of R_{Sx} by either substrate diffusion limitation (MM_{Sx}), or oxygen limitation (MM_{O2}). V_{max} is affected by temperature, and the two MM-terms are affected by soil water content (Figure S1a in Supporting Information S1). With this relatively simple framework and without explicitly simulating microbial biomass or activity, MM_{Sx} represents substrate diffusion to a microbial surface, while MM_{O2} represents oxygen availability. When either is limiting, R_{Sx} is reduced.

Following G. Wang et al. (2012), the Arrhenius function V_{max} is expressed as:

$$V_{max} = \alpha_{S_x} \cdot \exp\left[-\frac{Ea_{Sx}}{R}\left(\frac{1}{T_{soil}} - \frac{1}{T_{ref}} \right) \right] \tag{2}$$

where α_{S_x} is a base rate (mg C cm^{-3} soil h^{-1}; Sihi et al., 2018, 2020), Ea_{Sx} is the activation energy for substrate S_x (kJ mol^{-1}), R is the universal gas constant (kJ K^{-1} mol^{-1}), T_{soil} and T_{ref} are soil temperature and reference temperature (K), respectively.

Substrate diffusion limitation is calculated as:

$$MM_{Sx} = \frac{[S_x]}{kM_{S_x} + [S_x]}; \tag{3}$$

where $[S_x]$ (g cm^{-3}) is the soluble substrate concentration, calculated as a diffusivity function from $S_{x,tot}$ (g cm^{-3}), the total amount of substrate:

$$[S_x] = S_{x,tot} \cdot p_{S_x} \cdot D_{liq} \cdot \theta^3 \tag{4}$$

The substrate of interest (S_x) for this study is the SOC density (Section 2.2), p_{S_x} is the fraction of carbon substrate which is soluble, D_{liq} is the diffusion coefficient of the substrate in liquid phase, and θ is the volumetric soil moisture content.

Oxygen diffusion limitation (MM_{O2}) is calculated in a similar fashion:

$$MM_{O2} = \frac{[O_2]}{kM_{O_2} + [O_2]}; \tag{5}$$

where the oxygen concentration at the reaction site, $[O_2]$, is also calculated as a diffusivity function, using soil porosity and water content to calculate the air-filled pore space (Millington, 1959):

$$[O_2] = D_{gas} \cdot O_{2,airfrac} \cdot (\Phi - \theta)^{\frac{4}{3}} \tag{6}$$

where D_{gas} is the diffusion coefficient for oxygen in air, $O_{2,airfrac}$ is the fraction of oxygen in air (L O$_2$ L^{-1} air), and Φ is the soil porosity. kM_{S_x} (g C cm^{-3} soil) and kM_{O_2} (cm^{-3} O$_2$ cm^{-3} air) are the half-saturation or Michaelis-Menten constants of the reactions with the substrate and oxygen, respectively. All climate and soil data input variables are described in Section 2.2, and all parameter values taken from the modeling script provided by

Davidson et al. (2012) are listed in Table S1 in Supporting Information S1. To verify that the DAMM model is not only suitable for the top soil layers but applicable throughout the whole soil column, we successfully applied the model on a set of monthly observations at multiple depth intervals up to 1 m (0–15, 15–30, 30–50, 50–70, 70–100 cm, Gomez et al., 2002; Hicks Pries et al., 2017). A detailed description of the data and methods is included in the Text S1 in Supporting Information S1.

2.2. Climate and Soil Input Data

The DAMM model (Section 2.1) requires the following variables and parameters: Soil temperature (T_{soil}), soil moisture (θ), SOC density ($S_{x,\text{tot}}$) and soil porosity (Φ). Variables T_{soil} and θ are extracted from CMIP5 models (listed in Table S2 in Supporting Information S1). We analyze outputs for a historical period (1976–2005) and a future climate change period (RCP8.5; 2070–2099), similar to Berg et al. (2016). We select only those CMIP5 models with a spatial resolution of at least $1° \times 1.25°$, which contain layered monthly data for soil temperature and soil moisture for both simulation periods. SOC concentrations strongly decrease with soil depth (e.g., Section 3.2 in Blume et al., 2016), so for this study we assume that the majority of the microbial decomposition takes place in the top soil and limit our analysis to the first 100 cm of soil. To ensure sufficient climate information is available for each soil depth, we select only those CMIP5 models containing outputs for at least five soil layers between 0 and 1 m depth (Table S2 in Supporting Information S1).

Global SOC estimates and soil porosity data are taken from the global soil information database SoilGrids (https://soilgrids.org). In this study, we use SoilGrids v0.5.3 at 10 km spatial resolution (Hengl et al., 2014, 2017), taking the datasets' standard soil depths to 1 m (0–0.05, 0.05–0.15, 0.15–0.30, 0.30–0.60, 0.60–1, m depth respectively, Figure S2 in Supporting Information S1). SoilGrids' porosity is defined as saturated water content (*tetaS* in Hengl et al., 2019). Since both SoilGrids' porosity and the CMIP5 soil moisture values are model outputs, there are cases where the CMIP5 soil moisture value exceeds SoilGrids' porosity, which lead to numerical errors in Equation 6. Neither model output is considered correct or false, so in order to match these values the soil porosity is set to

$$\Phi = \max\left(tetaS, \max(\theta_{histo}, \theta_{RCP8.5})\right) \tag{7}$$

in each grid cell, where θ_{histo} and $\theta_{\text{RCP8.5}}$ are the monthly soil moisture contents during the historic and RCP8.5 simulation periods, respectively. In addition, a spatial mask is applied to exclude areas classified as hot or cold deserts, where the soil might be permanently dry or frozen and where SOC content and aboveground plant productivity are expected to be low. We mask grid cells following Carvalhais et al. (2014), excluding Köppen-classified hot and cold deserts and low GPP estimates (below 10 g C m^{-2} y^{-1}), as well as any grid cells containing NA's in one of the input datasets (soil moisture, soil temperature, porosity, SOC density).

2.3. Data Preprocessing

SOC stocks (ton C ha^{-1}) were converted to densities (g C cm^{-3}) at layer mid-point depth (0.025, 0.10, 0.225, 0.45, 0.8 m) after Hengl et al. (2017). SOC content, soil porosity and the mask were then spatially re-gridded to match the respective CMIP5 model spatial resolution (using raster::aggregate and raster::resample, method = 'bilinear'). Soil moisture (mrlsl) provided in kg m^{-2} was converted to volumetric water content (θ), using CMIP5 model soil layer thickness. Soil moisture and temperature data were vertically re-gridded to the midpoint depths of the five SoilGrids standardized depth intervals (0–5, 5–15, 15–30, 30–60, 60–100 cm), by computing the weighted average of the intersecting components of the CMIP5 model depth intervals. All analyses were done in RStudio (RStudio Team, 2018) using packages raster, ncdf4, pals, plyr, plotrix, and rgdal.

2.4. Model Experiment

We applied the DAMM model at five different depths (Section 2.2) and on each individual gridcell for the historical and RCP8.5 climate change scenario. Throughout the paper we investigate changes in R_{Sx} (a) considering the full DAMM model (Equation 1); (b) only considering the temperature-sensitive part of the DAMM model (V_{max}, Equation 2) and refer to this as the "T only" effect on the modeled decomposition rate; and (c) considering only the moisture-sensitive part of the DAMM model (the two MM-terms in Equations 3 and 5) and refer to this as the "SM only" effect on the modeled decomposition rate.

For each CMIP5 model, the changes in R_{Sx}, V_{max} and the two individual MM-terms (substrate limitation, MM_{Sx}: Equation 3 and oxygen limitation, MM_{O2}: Equation 4) are investigated further. First, to study the anticipated climate change effects (i.e., a warming and drying/wetting soil between locations and with depth), we calculate the relative change in modeled decomposition rates (change in R_{Sx}) between the historical period and the RCP8.5 scenario for each soil depth for the full DAMM model. Following Equation 1, for soil layer i:

$$\Delta R_{Sx,i} = \left(\frac{[V_{max} \cdot MM_{Sx} \cdot MM_{O2}]_{RCP8.5,i}}{[V_{max} \cdot MM_{Sx} \cdot MM_{O2}]_{histo,i}} - 1 \right) \cdot 100\% \tag{8}$$

Then, modeled changes in $V_{max,i}$ ("T only"), $MM_{Sx,i} \cdot MM_{O2,i}$ ("SM only"), and the two individual MM-terms are calculated in a similar fashion.

Throughout the paper we refer to drying or wetting of the soil between the two simulation periods as SM- or SM+, respectively. Similarly, decreases or increases in the modeled decomposition rates (Equation 8) are indicated as R- or R+, and changes in the MM terms for substrate and oxygen (Equations 4 and 5) as Sx-/Sx+ or O_2-/O_2+, respectively. As conceptually outlined in Figure S1b in Supporting Information S1 (black line), a soil moisture driven decomposition rate increase (R+) can be caused by either an increase in available substrate (Sx+) or an increase in oxygen availability (O_2+). Reversely, a decrease in decomposition rate (R-) can be caused by lower substrate or oxygen availability (Sx- and O_2-, respectively). Therefore, apart from presenting the global figures, we also present the contribution of the MM-terms to the directional change in decomposition rate (R) as a ratio (R+ ratio as S_x+: O_2+ or the R-ratio as S_x-: O_2-). A ratio of 1 indicates both MM-terms were equally important to the overall directional change in decomposition rate (R+ or R-); a value > 1 indicates a change in substrate availability was the dominant contributor; and a value < 1 indicates that oxygen availability was the dominant contributor. The global figures in this paper include a panel where the respective probability density distribution (PDF) of the modeled values is shown. Color bars are calculated using the 2nd to 98th percentile of the values (standardized across all four models).

2.5. Comparison of DAMM Model to Observations at Multiple Depths and Sensitivity Analyses

To demonstrate the applicability of the DAMM model for our modeling study, we compare the DAMM model to a set of soil respiration observations at different depths. Studies with a complete set of suitable data are extremely rare, but we found a deep mineral soil warming experiment in the USA which contained monthly measurements at multiple depths (up to 100 cm) needed as inputs for and validation of the DAMM model (Hicks Pries et al., 2017): Soil temperature, soil moisture, soil C content (measured once), and the observed soil C flux for comparison to modeled C fluxes. Soil porosity measurements at the site were additionally taken from Gomez et al. (2002). Hicks Pries et al. (2017) measured soil C flux (g C m^{-3} hr^{-1}), soil temperature, soil moisture at five mid-point depths: 7.5, 22.5, 40, 60, 80 cm. Soil C properties were measured at 10 cm depth intervals from 0 to 100 cm. Gomez et al. (2002) measured porosity at 15 cm depth intervals from 0 to 45 cm. Similar to Section 2.3, soil C stocks were recalculated to densities (g C cm^{-3}) and together with soil porosity calculated as a weighted average for each layer at the 5 midpoint depths.

To test the sensitivity of the DAMM model to different substrate and oxygen levels, we run the DAMM model on the observation data. We used the exact same moisture and temperature sensitivities as Davidson et al. (2012) (Table S1 in Supporting Information S1), only refitting the α_{Sx} parameter, which describes the base rate at a site (Sihi et al., 2018, 2020). We performed three model experiments: (a) A standard model run using the measured soil C content ($S_{x,tot}$, Equation 4), and the time series of measured soil moisture (θ), soil temperature (T_{soil}), and porosity (Φ) as inputs for each depth interval; (b) As run (a), but using a constant soil C content ($S_{x,tot}$ is set to the mean soil C density between 0 and 100 cm) for each soil layer to test how sensitive the model is to changes in substrate availability; and (c) As run (a), but we let $O_{2,airfrac}$ (Equation 6) decline from 0.21 to 0.04 to test how sensitive the model is to changes in oxygen availability. All analyses were done in RStudio (RStudio Team, 2018) using packages ModelMetrics and FME).

We also tested the sensitivity of the DAMM model with the CMIP5 model runs. As with the observation data set, we tested how sensitive the model is to changes in oxygen availability by letting $O_{2,airfrac}$ (Equation 6) decline from 0.21 to 0.04. Furthermore, by generating 1000 parameter vectors through latin hypercube sampling from a range between 80% and 120% of the original parameters (α_{Sx}, Ea_{Sx}, kM_{Sx} and kM_{O2}, Table S1 in Supporting

Information S1) as reported by Davidson et al. (2012), we also tested the sensitivity of DAMM to changes in these parameters in conjunction with the sensitivity to changes in substrate availability ($S_{x,\text{tot}}$) and to different initial soil moisture values (using constant $O_{2,airfrac}$ and $S_{x,\text{tot}}$ from Davidson et al. (2012)).

3. Results

3.1. Soil Temperature Effects on Modeled Decomposition Rates

All four CMIP5 models predict an overall rise in soil temperatures between the historical and RCP8.5 simulation periods of 2.8–4.2 K ($\Delta\overline{ST}$, Table S2 in Supporting Information S1). As a direct result, the temperature only effect, that is, the modeled maximum decomposition rate ($V_{\max}$), increases between the two simulation periods (Figure 1 and S3 in Supporting Information S1, T only). For all models, the top soil layers (0–5 cm) are exposed to stronger warming than the deepest soil layers (60–100 cm), especially in northern latitudes. Overall, the T only model predicts an increase in decomposition rates of 10%–120%, driven by rising soil temperatures alone. The predicted mean change in soil temperature ($\Delta\overline{ST}$) for models CESM1-BGC and NorESM-1M is 3.7 K, and Figure S1 in Supporting Information S1 conceptually shows how this mean temperature change affects the modeled decomposition rate. At optimum soil moisture, the T only effect is at its maximum.

3.2. Soil Moisture Effects on Modeled Decomposition Rates

The soil moisture-sensitive part of the DAMM model (the two MM-terms in Equations 3 and 5) changes the modeled decomposition rates in both directions. In other words, inclusion of soil moisture slows down or speeds up the modeled decomposition rates by up to 20% at the end of the century for all models (Figure 1 and S3 in Supporting Information S1, SM only). For the topsoil (0–5 cm), drying (SM-) generally leads to a reduction of decomposition rates (R-), and wetting (SM+) to an increase in decomposition rates (R+, Table 1). For the deeper soil layers, there is a different pattern: First, drying leads to an acceleration of decomposition more often in the deep soil (i.e., SM-/R+ occurs more frequently in deep soil compared to the top soil); and second, wetting leads to a slowdown of decomposition more often in the deep soil (i.e., SM+/R- occurs more frequently in deep soil compared to the top soil). Three out of four models show these patterns in the top- and deep soil layers; only INM-CM4 does not. INM-CM4 predicts relatively high overall mean soil moisture ($\overline{SM}$) and small changes ($\Delta\overline{SM}$) between the two simulation periods (Table S2 and Figure S4 in Supporting Information S1). So with overall wetter conditions, a (small) decrease in moisture is more likely to lead to higher oxygen availability rather than induce substrate limitation (Figure S1 in Supporting Information S1, and see Section 3.3).

3.3. Substrate and Oxygen Availability

In the top soil (0–5 cm), the modelled response of decomposition rates is mostly driven by changes in substrate availability (Figures 2 and S5 in Supporting Information S1, Table 2). The top- and middle panels of the figures show the individual effects of the two MM-terms (oxygen and substrate availability, Equations 5 and 3), as well as their combined effect on the modelled decomposition rate (SM only, bottom panel). In the the deeper soil layers (60–100 cm), oxygen limitation plays an increasingly large role: Reduction of oxygen availability (blue cells) increasingly corresponds to grid cells showing a slowdown of the decomposition rates. Table 2 summarizes these results for each model by showing the relative contribution of each MM-term (i.e., a change in substrate/oxygen availability) to the overall change in the modeled decomposition rate (R+/R-). There is a clear pattern between the top- and deep soil for the slowdown of decomposition (R-): The dominant contributor in the topsoil (0–5 cm) is a decrease in substrate availability (ratio > 1), whereas in the deep soil layer (60–100 cm) a reduction in oxygen availability (R-ratio < 1) is the dominant contributor for three out of four models. For all models, the contribution of oxygen limitation (O_2-) becomes more important towards a slowdown of decomposition in the deep soil (60–100 cm). And for model INM-CM4, oxygen availability generally contributes more often towards an acceleration of decomposition rates. This is related to the relatively high overall mean soil moisture ($\overline{SM}$) and small changes ($\Delta\overline{SM}$) between the two simulation periods for this model (Table S2 and Figure S4 in Supporting Information S1): When soil moisture is high and possibly close to saturation, drying would lift oxygen limitation and accelerate decomposition rates (Table 1, INM-CM4: SM-/R+, Figure S1b in Supporting Information S1). The opposite is true for for GFDL-ESM2M, where ($\overline{SM}$) and ($\Delta\overline{SM}$) are generally low (Table S2 and Figure S4 in Supporting Information S1), and therefore changes in substrate availability are always the dominant factor
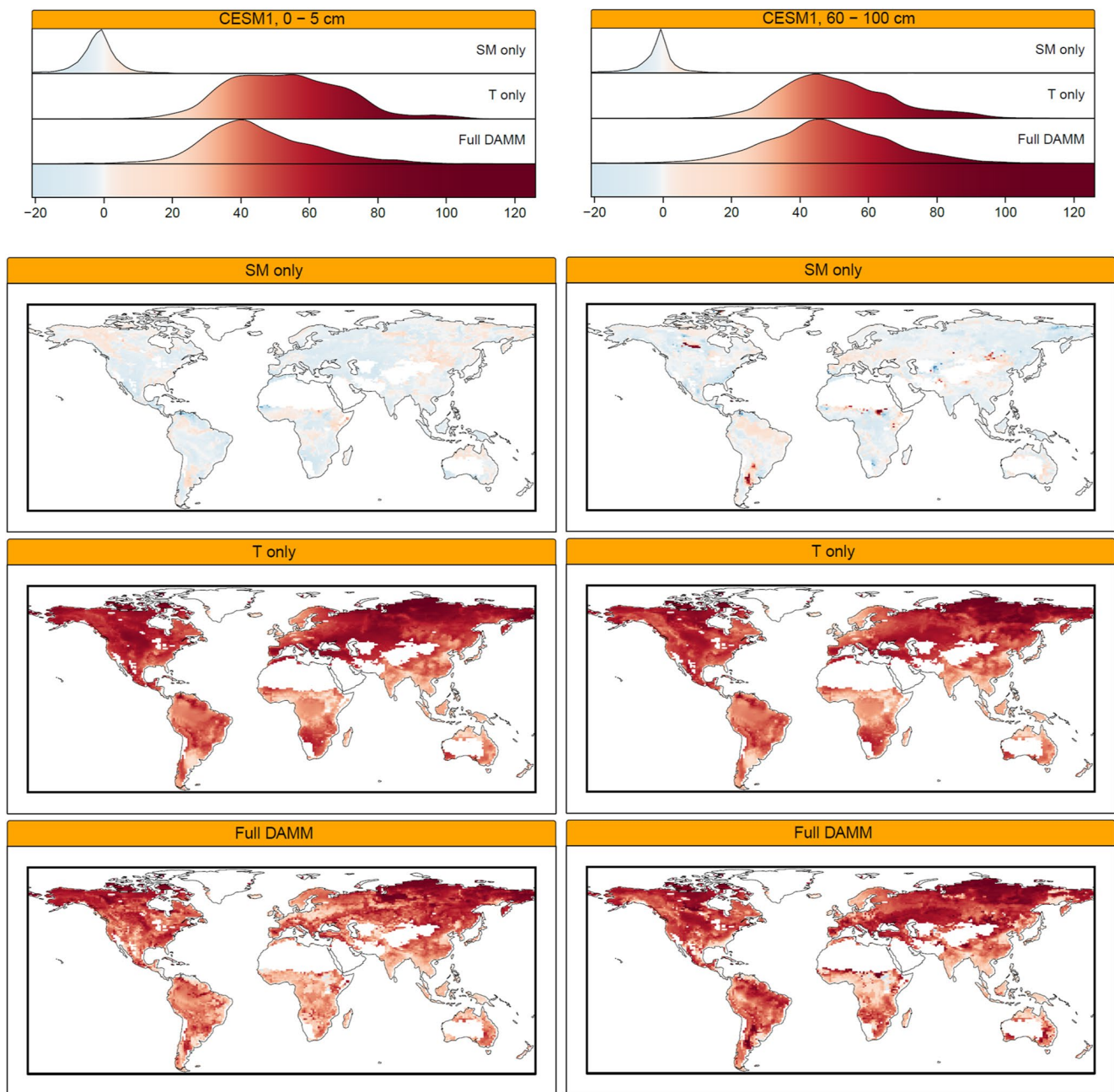
Figure 1. World maps showing changes in decomposition rate R_{Sx} in the topsoil (0–5 cm) and bottom soil layer (60–100 cm) for CMIP5 model CESM1-BGC, due to soil moisture changes (SM only); due to temperature changes (T only); due to soil moisture and temperature changes (Full Dual Arrhenius Michaelis-Menten). All units are in % and calculated as the change between the historic and RCP8.5 simulation period (Equation 8). Blue cells indicate a slowdown, and red cells indicate an acceleration of the modeled decomposition rate between the two simulation periods. Color saturation indicates the relative speed of de-/acceleration. The top panels show the corresponding probability density functions for the values displayed in each world map. Breaks for the color scale are calculated using the inner 98 percentile of values.

determining the modelled change in decomposition rate (Table 2). Generally, the majority of the changes in the modelled decomposition rates are driven by changes in substrate availability, especially for modelled accelerations of the decomposition speed (Table 2, R+ ratio). In the deeper soil layers, however, changes in oxygen availability become increasingly important for the overall response of decomposition rates to soil moisture.

Table 1

Summary of Soil Moisture Effects for All Four CMIP5 Models in the Topsoil (0–5 cm; 15–30 cm) and Subsoil (60–100 cm) Between the RCP8.5 and Historic Simulation Period

Model	Depth (cm)	SM- /R-	SM-/ R+	SM+/R-	SM+/ R+	no SM change
CESM1-BGC	0–5	46.4	6.4	19.5	27.7	0.0
	15–30	26.9	8.4	39.1	25.6	0.0
	60–100	16.6	13.2	50.0	20.2	0.0
INM-CM4	0–5	44.5	30.6	17.5	7.4	0.0
	15–30	30.5	34.9	25.2	9.4	0.0
	60–100	24.3	27.8	27.1	18.0	2.8
NorESM-1M	0–5	48.4	8.1	17.4	26.1	0.0
	15–30	29.7	11.1	35.7	23.5	0.0
	60–100	17.8	18.5	44.3	19.3	0.0
GFDL-ESM2M	0–5	47.1	19.0	9.0	24.9	0.0
	15–30	41.0	18.2	13.6	27.2	0.0
	60–100	41.7	21.4	14.4	22.3	0.2

Note. Numbers show the percentage of grid cells which became drier (SM-) or wetter (SM+) and whether this led to a slowdown (R-) or acceleration (R+) of the modelled decomposition rate (SM only). Two models predicted a small percentage of grid cells without soil moisture changes (no SM change).

3.4. Soil Moisture and Temperature Effects on Modeled Decomposition Rates

The full DAMM model (Figures 1 and S3 in Supporting Information S1, bottom panels), with the combined effects of soil temperature and soil moisture changes, generally follows the distribution of the T only response, but has a wider distribution of values that can be attributed to the soil moisture effect (top panels, SM only). In some cases, inclusion of soil moisture changes leads to a reversed direction of the predicted T only decomposition rates (Figures 1 and S3 in Supporting Information S1: Full DAMM, blue grid cells). All models show a wider PDF when soil moisture effects are included (Full DAMM): While this combined temperature and moisture effect still generally leads to a predicted acceleration of the decomposition rates at the end of this century, there is a shift toward more extreme values in both directions. For all models, and all depths, at least 52% of grid cells indicate a slowdown of decomposition in response to soil moisture changes (Table 2). A predicted slowdown occurs most frequently in the topmost soil layer (0–5 cm) lowering the overall mean predicted decomposition rate, often in response to soil drying (Table 2 and Figure S4 in Supporting Information S1). Typically, this also corresponds to soil layers where larger amounts of SOC are stored compared to the deeper layers (Figure S2 in Supporting Information S1). Deeper into the soil, the soil moisture response becomes more bi-directional, with increasing percentages of grid cells predicting an acceleration (Table 2).

3.5. Applicability and Sensitivity of the DAMM Model

To demonstrate the applicability of the DAMM model for our modeling study, we compared the DAMM model to a set of soil respiration observations at different depths. Our analysis shows that the DAMM model can be applied to vertically resolved respiration fluxes, using the same parameters and sensitivities to soil moisture as in our model experiment with the CMIP5 models (only calibrating α_{Sx}). The DAMM model is very sensitive to changes in substrate concentrations: When ran with a constant SOC value for each soil depth, the model is no longer able to capture the respiration fluxes at any given soil depth. The model was not very sensitive to changes in the oxygen fraction in air. A full description of the site-level study and results can be found in the Supporting Informations, Text S1 and Figure S6 in Supporting Information S1.

The sensitivity tests with the CMIP5 model data reveal that the modeled changes in decomposition rate due to changes in soil moisture are sensitive to the initial soil moisture conditions (Figure 3). The sensitivity range of the reaction rate to a ±20% change in the DAMM parameters is very small, and at most, falls between 2–5 percent change in reaction rate for larger changes in absolute water content. The potential for vertical divergence due to changes in soil moisture is visible: At low and high initial soil moisture content (ini. θ of 0.15 and 0.4), the modeled changes in the decomposition rates are largest, but have relative small uncertainties. For example, in a soil column with a dry top soil and a moist deep soil layer (ini. $\theta = 0.15$ and 0.4, respectively), the response of the modeled decomposition rate to a further drying or wetting would be opposing for both layers. As initial soil moisture comes closer to the DAMM model's optimum value (see Figure S1b in Supporting Information S1), there is less divergence in the modeled response of the reaction rate, but uncertainty increases slightly for larger changes in absolute water content (max. $\pm$ 3% change in absolute water content shown in Figure 3). The reported changes in modeled decomposition rates due to soil moisture changes in the CMIP5 models used for our study fall between −20% and 20% ("SM only" in Figures 1, 2, S3 and S5 in Supporting Information S1). In other words, our results would not drastically change if we consider the added uncertainty from both the DAMM parameters and initial soil moisture conditions.

Depending on initial soil moisture content, our results can be sensitive to SOC content ($S_{x,tot}$ from Equation 4, Figure S7 in Supporting Information S1). For dry and wet initial soil moisture conditions (ini. θ 0.15–0.2 and 0.35–0.4, respectively), there is little sensitivity of initial SOC content on the direction and magnitude of the modeled decomposition responses, but this increases for larger absolute changes in water content. Around the
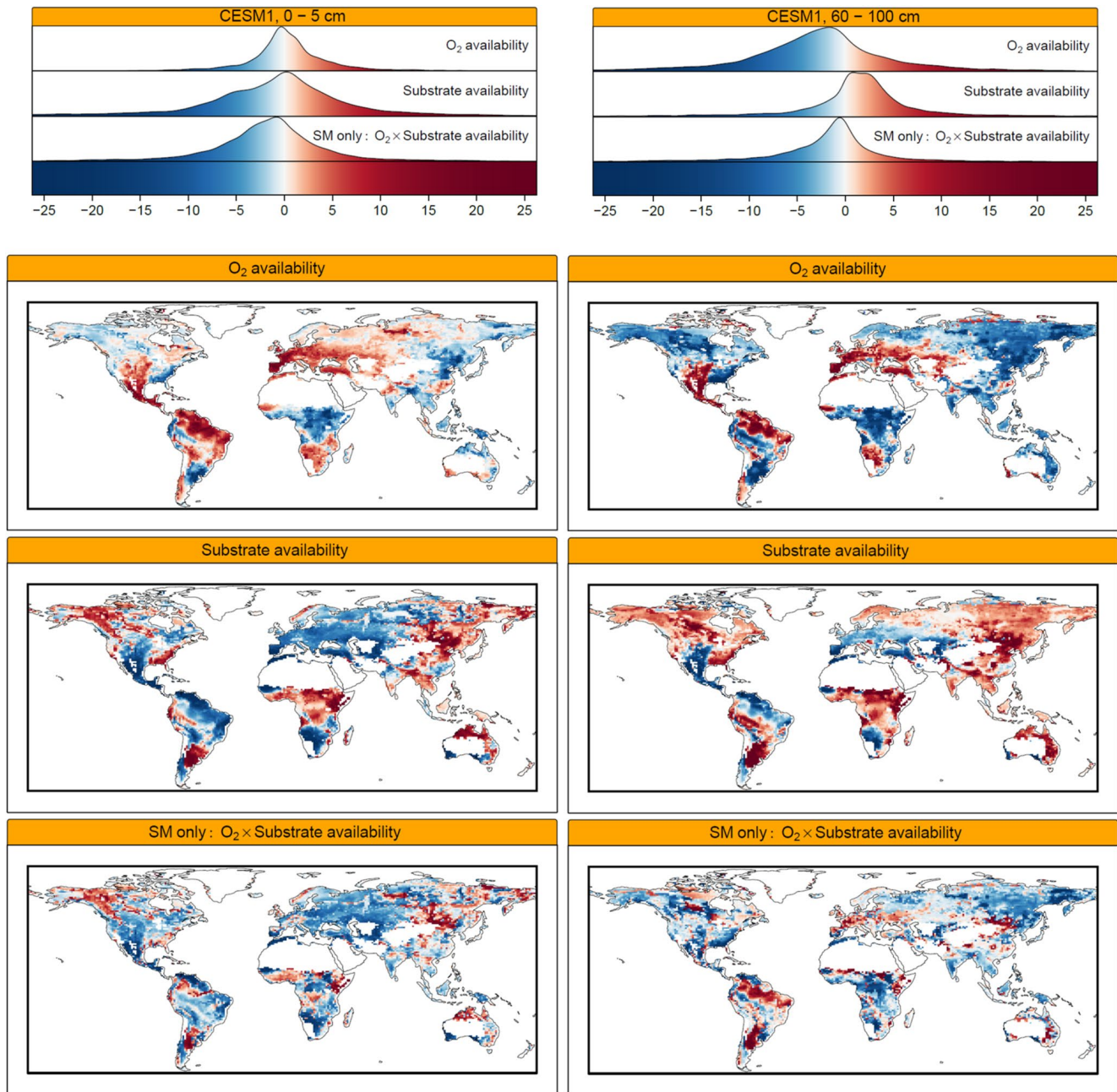
Figure 2. World maps showing changes in modeled decomposition rates R_{Sx} in the topsoil (0–5 cm) and bottom soil layer (60–100 cm) for CMIP5 model CESM1-BGC, due to changes in oxygen availability (top panel); due to changes in substrate availability (middle panel); and the combined soil moisture effect (SM only: $O_2 \times$ Substrate availability, bottom panel). Units and calculation of breaks, colors and saturation similar to Figure 1.

soil moisture optimum (ini. $\theta = 0.25$–0.3), there is a small additional vertical divergence visible due to changes in initial SOC content: For example, at an initial soil moisture content of 0.25, the decomposition rate is expected to decelerate in response to drying at low substrate levels ($S_{x,tot} = 0.01$–0.05 g C cm^{-3}), as a result of further restrictions of the substrate availability. But at higher substrate levels ($S_{x,tot} = 0.09$–0.11 g C cm^{-3}), the modeled decomposition rate accelerates in response to drying. So, depending on the initial soil moisture condition, future drying or wetting of a soil layer can lead to opposite effects depending on its SOC content. Generally, top soil layers have higher SOC contents than deeper layers, although this may be different in, for example, peat soils (blue areas in Figure S2 in Supporting Information S1, 60–100 cm).

Table 2

Summary of Combined and Individual MM-Terms' Effects on Decomposition Rates for Four CMIP5 Models in the Topsoil (0–5 cm; 15–30 cm) and Subsoil (60–100 cm) Between the RCP8.5 and Historic Simulation Period

Model	Depth (cm)	slowdown (%)	acceleration (%)	R- ratio (S_x- : O_2-)	R+ ratio (S_x+ : O_2+)
CESM1-BGC	0–5	75	25	2.28	4.40
	15–30	66	34	0.69	3.01
	60–100	64	36	0.33	1.51
INM-CM4	0–5	62	38	2.56	0.28
	15–30	56	44	1.24	0.30
	60–100	52	48	0.91	0.65
NorESM-1M	0–5	74	26	2.74	3.23
	15–30	66	34	0.84	2.10
	60–100	60	40	0.40	1.04
GFDL-ESM2M	0–5	57	43	4.99	1.34
	15–30	56	44	2.94	1.52
	60–100	58	42	2.83	1.03

Note. Slowdown and acceleration are the percentage of grid cells where soil moisture changes slowed down or accelerated the decomposition rate compared to T-only (Full DAMM < T-only; or Full DAMM > T-only, respectively). The ratio S_x: O_2 represents the relative contributions of the individual terms towards a slowdown (R-)/acceleration (R+), respectively. A ratio of 1 represents an equal contribution of both MM-terms; values > 1 indicate that substrate availability (S_x) contributed more often; values < 1 indicate that oxygen availability (O_2) contributed more often.

The sensitivity test with the CMIP5 model data and a linearly declining $O_{2,airfrac}$ from 0.21 to 0.04 at 1 m soil depth, indicates that our results have little sensitivity to such a steep decline in oxygen availability. Figure S8 in Supporting Information S1 shows the difference in percentage points between the standard CMIP5 model runs ($O_{2,airfrac}$ constant at 0.21) and the runs with linearly declining oxygen gradient (Section 2.5). As expected, the top soil layer (0–5 cm) is hardly affected and the deep soil layer is most affected, but the changes are small. For all models, 90% of all data points did not change more than 2 percentage points from the model runs as presented in the manuscript, which means our results would not have drastically changed had we additionally assumed vertically decreasing oxygen levels in the DAMM model.

4. Discussion

4.1. Bi-Directional Response of Decomposition Rates to Soil Moisture

Our results show that changes in soil moisture have the potential to slow down or speed up the predicted decomposition rates by as much as 20%, compared to up to more than a doubling of the decomposition rate due to warming alone (20%–110%). This bi-directional behavior is a direct result of the interplay between the multiplicative substrate and oxygen availability terms in the DAMM model (Figure S1b in Supporting Information S1): Both a soil drying or wetting can direct the decomposition rate toward an optimum or a further decrease. Despite the strong overall temperature response, all CMIP5 model outputs considered in this study resulted not only in regions with a slowdown but also an acceleration of decomposition rates following soil moisture changes (Figures 1 and S3 in Supporting Information S1). This contrasts with earlier work by for example, Falloon et al. (2011), who reported that temperature-driven decreases in soil carbon by the year 2100 tended to be opposed by soil moisture, implying a slowdown of conventional turnover rates in response to soil moisture. The sensitivity analyses of the DAMM model revealed that parameter uncertainty only influences the predicted decomposition rates by 2%–5% so that the observed trends are due to other factors discussed below. In our study the direction of expected changes in modeled decomposition rates at the end of this century depends on (a) the differences in the initial (historical) soil moisture levels in conjunction with (b) the projected soil moisture changes between CMIP5 models (Figure S4 in Supporting Information S1). Within the full CMIP5 model ensemble there is a large spread in model results for both, the initial soil model conditions, as well as the projected soil moisture changes under the RCP8.5 scenario (Berg et al., 2016; Cheng et al., 2017; Lorenz et al., 2016; Orlowsky & Seneviratne, 2013). We have shown the results for four different models of the CMIP5 ensemble to demonstrate the potential impacts of soil moisture on the modeled decomposition rates, where one model is on the drier end (GFDL-ESM2M), one on the wetter end (INM-CM4) and two models in the mid-range (CESM1-BGC and NorESM-1M). The bi-directional nature of the modeled decomposition rate response to soil moisture exists, however, for all models and at all soil depths.

Besides initial conditions, individual CMIP5 models also predicted different magnitudes and direction of soil moisture changes for each grid cell and also with depth, which was reported earlier by Berg et al. (2016). It is known that uncertainty in soil moisture projections between CMIP5 models is large, especially for near-surface soil moisture (Berg & Sheffield, 2018; Berg et al., 2016; Cheng et al., 2017; Lu et al., 2019; Yuan & Quiring, 2017). While climatic variability dominates differences in soil moisture predictions between CMIP5 models on shorter time scales, individual model formulations generally become the dominant source of model spread by the end of the 21st century (Orlowsky & Seneviratne, 2013). Our results show that for predicting future soil carbon it is also vital that the projections of soil moisture become better understood and constrained.
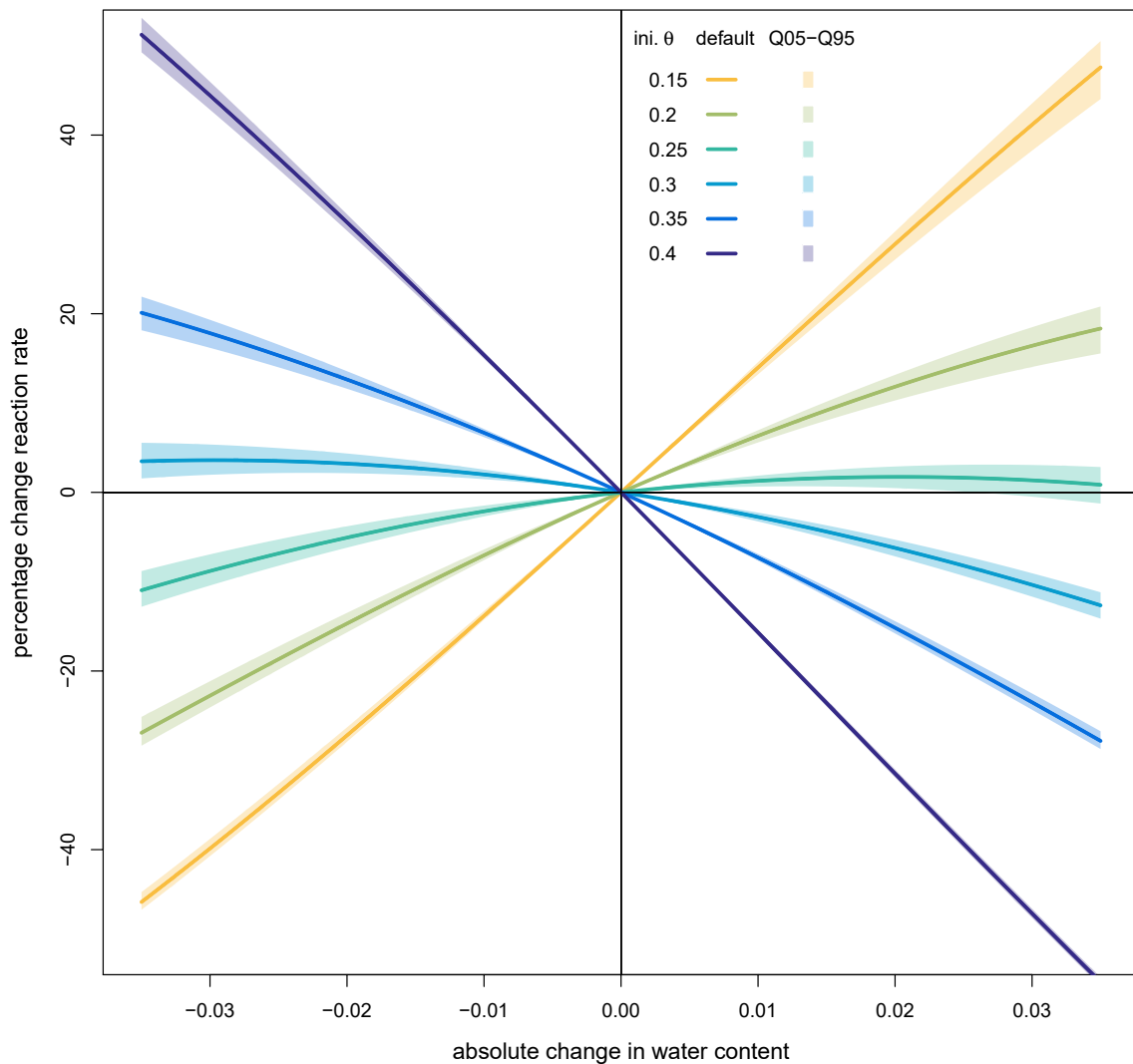
Figure 3. Sensitivity of Dual Arrhenius Michaelis-Menten (DAMM) model "SM only" to an absolute change in water content between the historic and RCP8.5 simulation period. Lines are colored for different initial soil moisture contents (ini. θ from 0.15 to 0.4). Shading represents the sensitivity range (Q05–Q95: 5th–95th percentile) to ±20% changes in the DAMM parameters used in this study (α_{S_x}, Ea_{S_x}, kM_{S_x} and kM_{O_2}, Table S1 in Supporting Information S1). CMIP5 models' historic mean soil moisture ranges from 0.24 to 0.29 (Table S2 in Supporting Information S1).

4.2. Vertically Divergent Response of Decomposition Rates to Soil Moisture

By considering the vertical distribution of soil moisture, we find that soil moisture changes can further accelerate the temperature-driven decomposition rate in ≥25% of the gridcells in the topsoil of the four different models (Table 2). This number increases to ≥34% in deeper soil layers due to the interplay of substrate and oxygen availability (Figure S1 in Supporting Information S1). Especially in the upper soil layers, substrate availability is the dominant factor for the overall response of decomposition rates to soil moisture changes in this study. Our results additionally show that a vertically varying profile of soil moisture and SOC content is very important for determining the direction and magnitude of changes in the decomposition rate in response to soil moisture changes. The sensitivity tests in Figures 3 and S7 in Supporting Information S1 clearly demonstrate the potential for a divergent model response due to changes in initial soil moisture content: For different initial values of soil moisture, the modeled decomposition rate can change sign for the same absolute change in water content. But additionally, initial values of SOC content can impact the sign of the modeled decomposition rate for the same absolute changes in water content when soil moisture is close to the optimum value (Figure S1 in Supporting Information S1). When the DAMM model was confronted with measured data (Figure S6 in Supporting Information S1), it could only reproduce the observed CO_2 fluxes well if a vertically varying SOC density was used.

Oxygen availability becomes increasingly important in the deeper soil layers. In our study we kept the amount of oxygen in the air-filled pore space ($O_{2,airfrac}$) at atmospheric concentrations (21%), so that we might underestimate oxygen limitation if oxygen consumption in the soil profile was not replaced by diffusion. The diffusion of oxygen depends on soil texture, structure, and porosity and to a less-known degree on organic matter content through its influence on aggregate stability and pore size distribution (Neira et al., 2015). However, our model results showed little sensitivity to a linearly declining $O_{2,airfrac}$ (Figure S8 in Supporting Information S1). As expected, the deepest soil layers were again the most affected: Soils that become wetter under future climate showed a possible, very small additional slowdown in response to reduced oxygen availability. The DAMM model does not explicitly simulate oxygen diffusion into and out of each soil layer, but indirectly simulates this by decreasing the decomposition rate due to water stagnation. Also, oxygen consumption during respiration could be an additional factor increasing anoxic conditions in soils, which is currently not considered in global scale SOC decomposition models. This possibly leads to an underestimation of the degree of anoxic conditions in soils, and would be a useful improvement when implementing DAMM into a SOC decomposition model.

Our results confirm the importance of including vertical gradients in SOC decomposition models, because top- and subsoil moisture projections can be highly divergent under future climate (Berg et al., 2016). Most existing SOC decomposition models consider only one soil depth with an average temperature and soil moisture change (Koven et al., 2017), and there are large differences between reported soil moisture values and projections when only the top 10 cm of the soil are considered versus a "whole column" approach (Berg et al., 2016). We demonstrate that SOC decomposition models which consider one soil depth with average SOC density, temperature, and moisture changes could poorly reflect the overall response of SOC turnover, because soil moisture at different depths can cause both accelerations and slowdowns of SOC turnover. So, while our study highlights the possible magnitude of decomposition rate changes with projected soil moisture (and temperature) changes, a quantitative assessment of the predicted changes in heterotrophic respiration and associated changes in SOC stocks additionally depends on the dynamic modeling of the feedback between climate change and SOC stocks (i.e., feedbacks of temperature and soil moisture on substrate availability, as well as fresh carbon inputs [NPP; Jian et al., 2021]).

4.3. Future Directions

Our study shows that soil moisture can have divergent effects on SOC decomposition rates, both in different parts of the globe, as well as with soil depth. The non-linear behavior and importance of temperature and water availability for soil carbon dynamics has been repeatedly shown in global data-driven and modeling studies with regard to carbon turnover rates (Carvalhais et al., 2014), decomposition rates (this study, Falloon et al., 2011; Sierra et al., 2015) and heterotrophic respiration rates (Tang et al., 2020; Zhou et al., 2008). Our study again highlights the importance of representing soil moisture controls on decomposition, but perhaps more importantly, on developing vertically resolved SOC decomposition models. Most commonly applied soil biogeochemical models use empirical soil moisture rate modifiers (SMRF) to reduce SOC turnover rates (Figure 4c in Sierra et al., 2015), but these do not provide insight into the potential mechanisms involved (Abramoff et al., 2017; Davidson et al., 2012; Fatichi et al., 2019; Moyano et al., 2018; Yan et al., 2018). The DAMM model represents a more mechanistic framework to the soil moisture effects on decomposition. While it does not explicitly simulate microbial biomass and enzyme production, it is designed to mimic the behavior of microbial decomposition of soil substrates in what can be considered a "big microsite representation" in the soil (Davidson et al., 2012, 2014). Microbes are the main actors of SOC decomposition, and their dynamics are affected by soil moisture through water potential (controlling their survival and function), and as a physical transport medium for the resources they consume. Both soil texture and structure influence soil moisture, which in turn affects the (de)sorption potential of SOC. The DAMM model partly, but not completely, represents these microbial processes in the form of substrate limitation and by using soil porosity as a proxy for soil pore structure. As microbes continuously change their behavior in response to soil drying and re-wetting, they alter soil carbon cycling at the ecosystem level (Schimel, 2018). Representing these mechanisms in more detail inside SOC decomposition models is therefore very important for improved estimates of future SOC turnover times (Jian et al., 2021). The DAMM equations provide one model representation of the interactions between microbes, SOC decomposition and soil temperature and moisture. But there are other sets of equations available that allow us to separate the individual effects of temperature and moisture on decomposition rates in a modeling environment: For example, Yan et al. (2018) added a co-location factor to account for the amount of spatial segregation between microbes and their substrate, and Ghezzehei

et al. (2019) suggested a representation using soil matric potential instead of volumetric soil water content, which can be more easily connected to plant- and microbe specific moisture gradients.

Our study shows that adding the vertical dimension is necessary to properly account for changes in substrate and oxygen availability. In our application of the DAMM model, the amount of SOC varies for each soil depth, which is important for a good representation of the potentially available substrate for decomposition. In the DAMM model, the amount of SOC that can go into solution is represented as a fixed fraction. In reality, however, an increasing contribution of SOC is not dissolved but sorbed to mineral surfaces with depth (Schrumpf et al., 2013), which can create a solubility gradient with depth and thereby modify the response to moisture. Furthermore, a depth-resolved modelling approach presents the advantage of representing other vital processes driving substrate availability: For example, entering root litter inputs at different depths, and capturing movement of organic matter between soil layers through leaching and bioturbation. Therefore, a depth-dependent SOC decomposition model should not only represent the microbially driven processes such as the DAMM model captures, but also consider plant inputs and SOC (de)sorption with depth (Ahrens et al., 2020; Soong et al., 2020). The integration of new scientific knowledge into SOC decomposition models can help build confidence in future soil carbon decomposition models (Wieder et al., 2019), even if increased model complexity comes with added uncertainty (Shi et al., 2018). In such modelling frameworks it will be possible to study the individual and joint effects of soil moisture controls on decomposition rates and test a variety of functions. A new generation of soil models should therefore be built in such a way that they represent the latest scientific insights and are designed as modular as possible to allow for mechanistic hypothesis testing (Fisher & Koven, 2020).

5. Conclusions

Future soil moisture changes are uncertain, but have the potential to both slow down or accelerate the predicted SOC decomposition rates at the end of this century. These slowdowns or accelerations will be mostly driven by changes in substrate availability, especially in the top soil. In the deeper soil layers, oxygen availability becomes increasingly important. Our study highlights that the development of the next generation of SOC decomposition models would benefit from including vertical representations of soil processes, with moisture sensitivity functions that reflect our mechanistic understanding of the effects of soil drying (and a reduction in substrate availability) and soil wetting (and the reduction of oxygen availability). Given the importance of SOC stocks in the overall C cycle, it is important such dynamics are integrated into the next generation soil models embedded in coupled global climate models. This would enable us to study the effects and potential feedbacks of soil moisture on SOC stocks and CO_2-release to the atmosphere under a changing climate.

Data Availability Statement

Soil carbon and porosity data can be downloaded from https://soilgrids.org, climate data are available at https://esgf-node.llnl.gov. Supporting R-script including our use of the DAMM model can be downloaded from https://gitlab.com/MarleenPallandt/pallandt_etal2021_jgrbg_decomposition_sm_response, which is permanently stored under a DOI: https://doi.org/10.5281/zenodo.5654554.

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