

Radiocarbon analysis reveals underestimation of soil organic carbon persistence in new-generation soil models

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Key Points:

- New-generation soil models generally overestimate ¹⁴C content in topsoil.
- This may be because new-generation models have too fast turnover rates and do not include highly persistent compounds such as pyrogenic carbon.
- Discovery of more representative measurable pools is likely to improve new-generation model designs and performances with ¹⁴C.

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Abstract

Reflecting recent advances in our understanding of soil organic carbon (SOC) turnover and persistence, a new generation of models increasingly makes the distinction between the more labile soil particulate organic matter (POM) and the more persistent mineral-associated organic matter (MAOM). Unlike the typically poorly defined conceptual pools of traditional SOC models, the POM and MAOM pools can be directly measured for their carbon content and isotopic composition, allowing for pool-specific data assimilation. However, the new-generation models' predictions of POM and MAOM dynamics have not yet been validated with pool-specific carbon and ^{14}C observations. In this study, we evaluate 5 influential and actively developed new-generation models (CORPSE, Millennial, MEND, MIMICS, SOMic) with pool-specific and bulk soil ^{14}C measurements of 77 mineral topsoil profiles in the International Soil Radiocarbon Database (ISRaD). We find that all 5 models consistently overestimate the ^{14}C content ($\Delta^{14}\text{C}$) of POM by 67‰ on average, and 3 out of the 5 models also strongly overestimate the $\Delta^{14}\text{C}$ of MAOM by 74‰ on average, indicating that the models generally overestimate the turnover rates of SOC and do not adequately represent the long-term stabilization of carbon in soils. These results call for more widespread usage of pool-specific carbon and ^{14}C measurements for parameter calibration, and may even suggest that some new-generation models might need to restructure their simulated pools (e.g. by adding inert pools to POM and MAOM) in order to accurately reproduce SOC dynamics.

1 Introduction

The terrestrial carbon reservoir sequesters an estimated 29% of anthropogenic CO_2 emissions each year (Friedlingstein et al., 2022), significantly reducing the accumulation rate of CO_2 in the atmosphere and thus slowing down climate change. However, the future role of the terrestrial carbon reservoir as a net CO_2 sink is uncertain, as Earth System Models (ESMs) produce a wide range of projections for the net land-atmosphere carbon flux over the course of the 21st century, partly due to high uncertainties in the carbon-climate feedback (Friedlingstein et al., 2014; Arora et al., 2020). Moreover, a study by He et al. (2016) using the radiocarbon (^{14}C) isotope suggests that some of the most widely used CMIP5 (Coupled Model Intercomparison Project Phase 5) ESMs may be systematically overestimating the future land carbon sink, further casting doubt on the reliability of future land sink predictions. All five ESMs tested in their study strongly underestimated the ^{14}C age of soil organic carbon, which indicates an overestimation of the simulated carbon cycling rates, particularly in the most stable soil carbon pools. After He et al. (2016) adjusted the soil carbon cycling rates to fit the observed ^{14}C data, the ESMs ended up predicting $40 \pm 27\%$ lower carbon sequestration by the terrestrial sink in the 21st century than with their default parameters. This result puts into question the ability of current ESMs to accurately model soil carbon dynamics, and highlights the importance of validating model predictions with ^{14}C data.

Almost all ESMs rely on soil organic carbon (SOC) modules that are ultimately based either on the Century model (Parton et al., 1987) (e.g., CESM2, Danabasoglu et al., 2020) or the RothC model (Coleman & Jenkinson, 1996) (e.g., JULES, Clark et al., 2011). Even though Century and RothC have been used for many decades to predict SOC dynamics in various landscapes with moderate success (Leifeld et al., 2008; Leifeld, 2008; Leifeld et al., 2009; Abramoff et al., 2022; H. Zhang et al., 2020), both modeling frameworks were developed in the 1980s, and thus reflect the comparatively limited understanding of soil carbon cycling of that time. Indeed, the model design of RothC is inspired by the now obsolete humification theory (Lehmann & Kleber, 2015; Schmidt et al., 2011), and neither RothC nor Century explicitly simulate specific processes of SOC cycling, such as physico-chemical protection of SOC or adsorption and desorption of dissolved organic carbon, because their mechanisms were previously not understood well enough.

According to our current understanding, the most important control on SOC stability is not so much the molecular composition or “quality” of organic matter, but rather its protection from microbial and abiotic decomposition through occlusion in aggregates and mineral association (Kleber et al., 2011; Dungait et al., 2012; Lehmann & Kleber, 2015; Lavalée et al., 2020). When SOC gets enclosed into aggregates or stabilized onto soil mineral surfaces through the action of pedogenic oxides, in particular iron, aluminum and calcium associated with clay particles (Rasmussen, Heckman, et al., 2018; Rowley et al., 2018; Vogel et al., 2014), it becomes less accessible to decomposers and thus significantly increases its residence time in soils (Basile-Doelsch et al., 2020; Schrumpf et al., 2013; Doetterl et al., 2015). A new generation of SOC models is now being developed to incorporate the theory of SOC protection through occlusion and interactions with soil minerals into our carbon cycle predictions. A common feature of new-generation soil models is their distinction between particulate organic matter (POM) and mineral-associated organic matter (MAOM). The POM pool largely consists of partially decomposed litter fragments smaller than 2 mm (Lavalée et al., 2020; Basile-Doelsch et al., 2020), which are usually covered with a thin mineral coating (Wagai et al., 2009). On the other hand, the MAOM pool contains organic matter chemically adsorbed onto reactive mineral surfaces, as well as strongly bound micro-aggregates formed around sand, silt, or clay particles (Basile-Doelsch et al., 2020; Lavalée et al., 2020). Unlike the carbon pools of RothC and Century, the POM and MAOM pools of the new-generation models can be operationally defined with experimental protocols by which they can be separated from soil samples and then analyzed individually for their elemental and isotopic composition (von Lützow et al., 2007). This allows for a closer look into the processes governing soil carbon stabilization and for potentially much larger datasets for model calibration and validation. However, the use of pool-specific measurements to validate models is still limited, even for new-generation models (Y. Zhang et al., 2021, Table S1).

The theory that protection and accessibility are the most important controls on SOC stability is strongly supported by ^{14}C studies (Gaudinski et al., 2000; Schrumpf et al., 2013, 2021), which could indicate that new-generation SOC models might perform better with ^{14}C than the traditional SOC models integrated into ESMs. ^{14}C is an effective carbon cycle tracer because it is chemically indistinguishable from the other carbon isotopes and therefore participates in the same carbon exchange mechanisms as the more abundant ^{12}C and ^{13}C isotopes. Over the past century, the atmospheric ^{14}C levels have undergone dramatic changes, most notably as a result of thermonuclear weapons tests in the 1950s and '60s, which have almost doubled the amount of atmospheric $^{14}\text{CO}_2$ in the Northern Hemisphere (see Figure 2). As this bomb-derived $^{14}\text{CO}_2$ spreads into the terrestrial carbon reservoirs through photosynthesis and into oceans through air-sea gas exchanges (Graven et al., 2020), the level of enrichment in bomb-derived ^{14}C across different terrestrial and oceanic carbon reservoirs helps to evaluate the speed and magnitude of carbon exchanges with the atmosphere on annual and decadal scales. Meanwhile for slower-cycling reservoirs such as deep soils or permafrost, the level of ^{14}C depletion due to radioactive decay (half-life of 5700 ± 30 years (Roberts & Southon, 2007)) helps to estimate the time scales of carbon stabilization in those reservoirs on the order of centuries and millennia. ^{14}C is therefore a powerful tool to study the exchanges and storage of carbon from decadal to millennial time scales. However, new-generation models do not generally implement ^{14}C simulations, and only a handful have systematically assimilated observed ^{14}C data (e.g., Tipping & Rowe, 2019; Braakhekke et al., 2014; Ahrens et al., 2020).

In this study, we use ^{14}C measurements of the organic carbon in the mineral topsoil to evaluate the performance of five new-generation SOC models: CORPSE (Sulman et al., 2014), MEND-new (G. Wang et al., 2022), Millennial v2 (Abramoff et al., 2022), MIMICS-CN v1.0 (Kyker-Snowman et al., 2020), and SOMic 1.0 (Woolf & Lehmann, 2019). These models were chosen because they are open source, actively developed, and influential in the soil modeling community. Leveraging the measurability of their pools,

we compare these models' predictions to ^{14}C measurements of POM and MAOM, in addition to the total soil ^{14}C . This provides a detailed picture of the modeled SOC dynamics and enables us to carry out an in-depth analysis of the models' performances.

2 Methods

Throughout this paper, we report the ^{14}C content of a given carbon sample as $\Delta^{14}\text{C}$, which is the deviation of the sample's $^{14}\text{C}/^{12}\text{C}$ ratio from the "modern" standard, corresponding to the pre-industrial atmospheric $^{14}\text{CO}_2/^{12}\text{CO}_2$ ratio (Trumbore et al., 2016).

2.1 Pool-specific carbon and radiocarbon measurements

We compare model predictions to three types of measured data for the topsoil: (1) the total SOC stocks in the topsoil, (2) the relative mass contributions of POM and MAOM to the total SOC stocks, and (3) the $\Delta^{14}\text{C}$ of POM, MAOM, and bulk SOC.

For this study, we will use the International Soil Radiocarbon Database (ISRaD) (Lawrence et al., 2020) for carbon and ^{14}C measurements of POM and MAOM obtained from soil samples using a combination of density fractionation and ultra-sonication. Density fractionation with ultra-sonication is currently one of the most effective and commonly employed methods for separating POM and MAOM (Golchin et al., 1994; Griepentrog et al., 2015, 2014; Cerli et al., 2012; von Lützow et al., 2007; Poeplau et al., 2018). This method separates the soil into three "density fractions" – the free light fraction, occluded light fraction, and heavy fraction – in a three step process: (1) obtain the free light fraction from the soil sample by density fractionation; (2) in the remaining sample, destroy loosely-bound aggregates with ultra-sonication, thus releasing the occluded fraction; (3) isolate the occluded light fraction from the relatively denser heavy fraction by density fractionation. The resulting free and occluded light fractions correspond approximately to the POM pool, while the heavy fraction is a good proxy for the MAOM pool (Mikutta et al., 2019; Lavalley et al., 2020). We will from now on refer to the soil density fractions (light and heavy) by the names of the corresponding pools (POM and MAOM, respectively).

ISRaD provides carbon and ^{14}C data for the bulk soil, and the free light, occluded light, and heavy fractions. We derive the relative carbon contributions and $\Delta^{14}\text{C}$ of POM with a weighted average of the free and occluded light fractions, and we directly associate MAOM with the heavy fraction in ISRaD. When the $\Delta^{14}\text{C}$ of the bulk soil is not measured or reported in ISRaD, we calculate it with a weighted average of POM $\Delta^{14}\text{C}$ and MAOM $\Delta^{14}\text{C}$. Since most of the available ^{14}C data is for the topsoil, we will evaluate models only for the top 5 cm or top 10 cm of the mineral soil. The current version of ISRaD (v 2.5.5.2023-09-20) contains complete ^{14}C datasets of the POM and MAOM density fractions in the topsoil of 77 soil profiles spread across 39 sampling sites, covering forests, shrubland, cultivated landscapes, and rangeland and grassland. Almost all of the sampling sites are in North America and Europe, and the remaining sites are located in Hawaii and Puerto Rico (see map in Figure 1). The dataset does not contain any permafrost, thermokarst, peatland, or wetland soils, and 75 of the 77 samples are from 1997-2015, with only one sample from 1949 and one sample from 1978. As shown in Figure 2, most datapoints bear a positive $\Delta^{14}\text{C}$ value, demonstrating an enrichment in bomb-derived ^{14}C in the topsoil.

2.2 Selection of new-generation models

We reviewed the literature to find new-generation models whose pools are fully compatible with the observed POM and MAOM density fractions, and that have already been tested with a range of soil types and environments. Table 1 gives an overview of the features and capabilities of such new-generation models, almost all of which have been de-

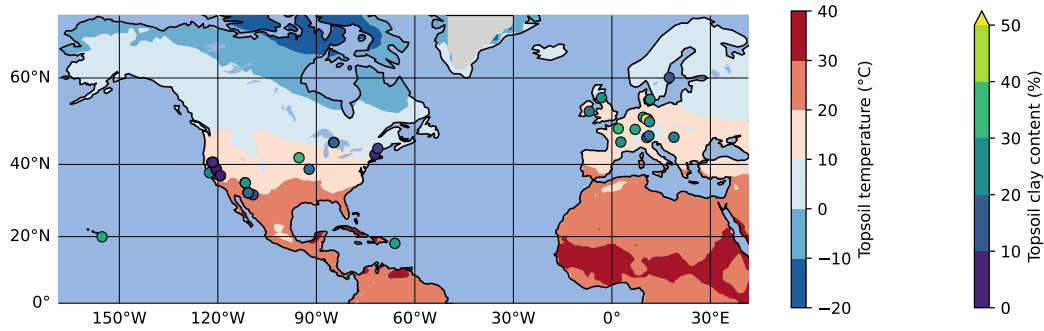


Figure 1. Map of selected topsoil sampling sites from ISRaD (Lawrence et al., 2020). 37 of the 39 sites are located in North America and Europe, and the two remaining sites are in Hawaii and Puerto Rico. All sites have a complete ^{14}C dataset for bulk soil and all density fractions for the top 5 or 10 cm of the mineral soil. The map also shows two of the most important environmental controls on soil carbon persistence: soil temperature (at 4 cm depth, averaged over 1970-2010 period, 1 degree horizontal resolution) from the CESM2 Large Ensemble product (Rodgers et al., 2021) on the map background, and clay content in the topsoil from ISRaD or SoilGrids (Poggio et al., 2021) for each sampling site.

veloped starting in the 2010s. Many new-generation SOC models also explicitly represent the microbial biomass as a separate carbon pool, since microbes are the main drivers of SOC turnover (Crowther et al., 2019; Basile-Doelsch et al., 2020; Schimel, 2023). The newest version of the MEND model simulates a variety of microbial exo-enzyme pools in addition to its microbial biomass pools (G. Wang et al., 2022). About half of the models listed in Table 1 have already been implemented with ^{14}C . However, none of them have systematically assimilated fraction-specific ^{14}C data, instead relying on ^{14}C data of bulk SOC or $^{14}\text{CO}_2$ data from soil respiration.

For this ^{14}C study, we chose to evaluate the following models, as their code is open-source and they have produced successful SOC predictions for a variety of ecosystems:

- Millennial v2 (with Michaelis-Menten kinetics), Abramoff et al. (2022),
- SOMic 1.0, Woolf and Lehmann (2019),
- MEND-new (with default equations), G. Wang et al. (2022),
- CORPSE (version from GitHub repository bsulman/CORPSE-fire-response), first described in Sulman et al. (2014),
- MIMICS-CN v1.0, Kyker-Snowman et al. (2020).

Figure 3 shows the general structure of the above models. All the selected models have pools which we can associate to the POM and MAOM fractions (see section S2 in the Supporting Information for details on how we associate the pools to each fraction), and they all have at least one microbial biomass pool. We generally chose to evaluate the most recent version of each model. However, we found an error in the ^{14}C implementation of the most recent version of MIMICS (Y. Wang et al., 2021) (see section S4.2 in the Supporting Information), so we chose to use the coupled carbon-nitrogen version MIMICS-CN published one year prior in Kyker-Snowman et al. (2020). See section S1 and Figures S1-S5 in the Supporting Information for more details on the exact versions and implementations of each model.

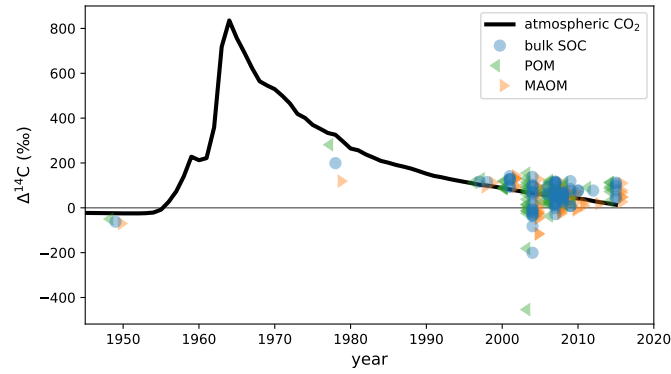


Figure 2. Measured $\Delta^{14}\text{C}$ data of the POM and MAOM density fractions and total soil organic carbon (SOC) at the selected topsoil profiles from ISRaD (Lawrence et al., 2020), overlaid on the atmospheric $\Delta^{14}\text{CO}_2$ curve of the Northern Hemisphere (Graven et al., 2017). All POM and MAOM fractions shown here were produced using the method of density fractionation with ultra-sonication. These ISRaD data were originally published in Baisden et al. (2002); Berhe et al. (2012); Harden et al. (2002); Heckman (2010); Heckman et al. (2018); Lybrand et al. (2017); Marín-Spiotta et al. (2008); McFarlane et al. (2013); Meyer et al. (2012); Rasmussen, Throckmorton, et al. (2018); Schrumpf et al. (2013).

Note that the MIND model (Fan et al., 2021) would have been a great candidate for evaluation, too, but only a subset of the modeled pools was run globally, so some of its parameters (e.g. $V_{\max,P}$ and $K_{M,P}$) do not have fitted values outside of 4 experimental test cases.

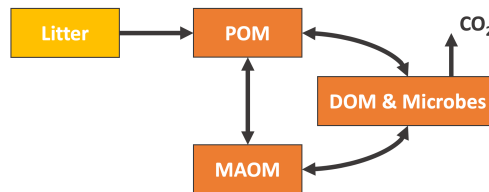


Figure 3. General structure of the new-generation models which we chose for this study. The MIMICS and CORPSE models additionally feature a CO_2 flux leaving MAOM and POM, which depends on the carbon use efficiency of the microbes. The SOMic and CORPSE models do not allow any flux from the DOM, Microbe, or MAOM pools back into the POM pool. More detailed diagrams for the MEND, Millennial, SOMic, CORPSE, and MIMICS models can be found in the Supporting Information (Figures S1-S5). Abbreviations: POM = particulate organic matter ; MAOM = mineral-associated organic matter ; DOM = dissolved organic matter.

2.3 Model input data

For each measurement site, the models are run with local environmental forcing data from 1850 to 2014. The initial conditions in 1850 are found by spinning up the models, looping over a “pre-industrial” year, where the forcing data is averaged over the 1850-1879 period, until the system reaches equilibrium, i.e. does not experience any signifi-

Table 1. Summary of features and capabilities of new-generation models. All of the listed models are compatible with the distinction between POM and MAOM and have been used to produce predictions for a variety of soil profiles. The models selected for evaluation with ^{14}C in this study are indicated with an asterisk (*). The first two columns are the year of the first publication and, if applicable, the year of the latest published revision of each model at the time of writing. The “Open-source,” “Implements ^{14}C ,” and “Explicitly models” columns are checkmarked if at least one version of the model has open-source code, implements ^{14}C simulations, or explicitly models a specified pool or feature, respectively. In the “Vertical mixing” subcolumn, models with a downward arrow (\downarrow) simulate any kind of downward transport or leaching for at least one of their pools, often in dissolved form, and sometimes using an advection equation. Models featuring an up-down arrow (\updownarrow) additionally implement vertical mixing for at least one of their pools with a diffusion equation.

Model name	First publication	Latest revision	Open-source	Implements ^{14}C	Explicitly models				Notes
					DOM	Microbes	Enzymes	Vertical mixing	
* Millennial ¹	2018	2022	✓		✓	✓		\downarrow	
* SOMic ²	2019		✓	✓	✓	✓		\downarrow	
* MEND ³	2013	2022	✓	✓	✓	✓	✓		^{14}C only in 2015
* CORPSE ⁴	2014	2020	✓			✓			
* MIMICS ⁵	2014	2021	✓	✓		✓		\updownarrow	^{14}C and \updownarrow only in 2021
MIND ⁶	2021		✓			✓			
AggModel ⁷	2013		✓						incubation model
JSM ⁸	2020		(✓)	✓	✓	✓		\updownarrow	source code accessible upon request
COMISSION ⁹	2015	2020		✓	✓	✓		\updownarrow	^{14}C introduced in v2.0
Tipping & Rowe ¹⁰	2019			✓	✓			\downarrow	
MEMS ¹¹	2019	2021			✓	✓		\updownarrow	\updownarrow introduced in v2.0
SOMPROF ¹²	2011	2014		✓				\updownarrow	^{14}C introduced in 2014
CAST ¹³	2013							\downarrow	
Struc-C ¹⁴	2009								
PROCAAS ¹⁵	2020								incubation model

¹Abramoff et al. (2018, 2022) ; ²Woolf and Lehmann (2019) ; ³G. Wang et al. (2013, 2015, 2022) ; ⁴Sulman et al. (2014, 2017); Salazar et al. (2018); Hicks Pries et al. (2018); Moore et al. (2020) ; ⁵Wieder et al. (2014, 2015); H. Zhang et al. (2020); Kyker-Snowman et al. (2020); Y. Wang et al. (2021) ; ⁶Fan et al. (2021) ; ⁷Segoli et al. (2013) ; ⁸Yu et al. (2020) ; ⁹Ahrens et al. (2015, 2020) ; ¹⁰Tipping and Rowe (2019) ; ¹¹Robertson et al. (2019); Y. Zhang et al. (2021) ; ¹²Braakhekke et al. (2011, 2013, 2014) ; ¹³Stamati et al. (2013) ; ¹⁴Malamoud et al. (2009) ; ¹⁵Liu et al. (2020)

cant inter-annual variability. More details on the spinup methods for each model are given in section S1 in the Supporting Information.

The selected models require a number of constant and time-dependent forcing data to be run at each study site. We assume that soil properties such as sand, clay and silt content, soil density, and land use are time-invariant since pre-industrial times. Where these site-specific soil properties are not reported in ISRaD, they are taken from the Soil-Grids database (Poggio et al., 2021). The MIMICS model also requires the lignin content of litter inputs, which we set to be a constant value depending only on the land use type. We assume that the lignin content is 25% for forest litter and 7% for shrubland litter (Rahman et al., 2013, Table 1). For grassland and cultivated landscapes, we assume a lignin content of 9% based on measurements of grasses at the seeding stage (Armstrong et al., 1950, Table 1). Weather-dependent and other dynamic environmental properties, such as soil temperature and ^{14}C influx, are taken from global model predictions with monthly time resolution. We use the monthly averaged CESM2 Large Ensemble (CESM2-LE) product (Rodgers et al., 2021) for vertically resolved soil temperature and moisture, above- and below-ground net primary production (NPP), total gross primary productivity (GPP), and the carbon-to-nitrogen ratio and $\Delta^{14}\text{C}$ of total litter carbon from 1850 to 2014 with 1 degree spatial resolution. Since the below-ground NPP from the CESM2-LE output is not vertically resolved, we derive the topsoil portion of the below-ground NPP using the exponential function model from Xiao et al. (2023). For nitrogen deposition rates, we use monthly data simulated by the NCAR Chemistry-Climate Model Initiative (CCMI) on a 0.5 degree grid from 1860 to 2016 (Tian et al., 2018). We extend this data back to 1850 by setting the monthly nitrogen deposition rates for the 1850-1860 period to be equal to the average monthly rates over the 1860-1870 period.

Since none of the selected models represent lateral carbon transport or upward vertical mixing of soil carbon, the simulated topsoil systems receive all of their carbon exclusively from vegetation inputs. We can therefore estimate the carbon influx into the soil with the NPP, and the $\Delta^{14}\text{C}$ of the influx with the $\Delta^{14}\text{C}$ of litter from the CESM2-LE product. In the case of the MEND model, we use GPP instead of NPP as a model input, as prescribed by MEND’s developers.

3 Results

We produced carbon and ^{14}C predictions with the MEND, Millennial, SOMic, CORPSE and MIMICS models for the 77 selected soil profiles, and compared them to the observed carbon and ^{14}C data from ISRaD. Our main performance metrics are the root mean squared error (RMSE) and mean bias of the predictions with respect to the 6 observational datasets described in Section 2.1. Table 2 gives a summary of the model performances, and Figures S8-S12 in the Supporting Information show plots of predictions against observations for each variable and each model. Note that the MEND model failed to run on 12 of the 77 selected soil profiles due to some numerical instability, and was unable to produce ^{14}C data for 3 other profiles. Note also that the SOC stocks for 17 of the 77 selected profiles are not available in ISRaD.

3.1 Carbon stocks and partitioning between pools

The SOMic, Millennial, and CORPSE models tend to overestimate the topsoil SOC stocks of the selected soil profiles, while MEND and MIMICS underestimate the SOC stocks, as shown in Figure 4a. In their predictions of SOC partitioning into POM and MAOM, the new-generation models generally fail to cover the full range of variability in the observations, with the exception of the MIMICS model (see Figure 4b-c). The CORPSE and MIMICS models perform the best, and both have a RMSE of around 20 percentage points, and a bias of around 10 points or less in magnitude. Meanwhile, the remaining models have an average RMSE of 35 points and an average absolute bias of around 25 points in their predictions of POM and MAOM contributions to total SOC stocks (see Table 2).

Table 2. Root mean squared error (RMSE) and mean bias for each model and each dataset. In the case of the MEND model, the RMSE and bias were calculated based on results of $n = 62$ profiles for the $\Delta^{14}\text{C}$ rows, $n = 52$ for SOC stocks, and $n = 65$ for the rows of POM and MAOM contributions. For all other models, $n = 77$ for all rows, except SOC stocks, where $n = 60$.

		MEND	Millennial	SOMic	CORPSE	MIMICS	Average
Bulk SOC $\Delta^{14}\text{C}$ (‰)	RMSE	84	115	101	90	80	94
	Bias	+59	+69	+46	+35	0	+42
POM $\Delta^{14}\text{C}$ (‰)	RMSE	94	120	100	119	129	112
	Bias	+50	+63	+56	+86	+80	+67
MAOM $\Delta^{14}\text{C}$ (‰)	RMSE	103	117	102	83	74	96
	Bias	+83	+82	+57	-3	-39	+36
SOC stocks (kgC/m^2)	RMSE	4.1	3.8	3.2	6.2	2.3	3.9
	Bias	-1.3	+2.7	+1.9	+4.0	-1.6	+1.1
POM contribution (%)	RMSE	35	40	32	23	17	29
	Bias	+24	-33	-22	+11	-2	-4
MAOM contribution (%)	RMSE	35	41	30	21	21	30
	Bias	-24	+35	+20	-9	-9	+2

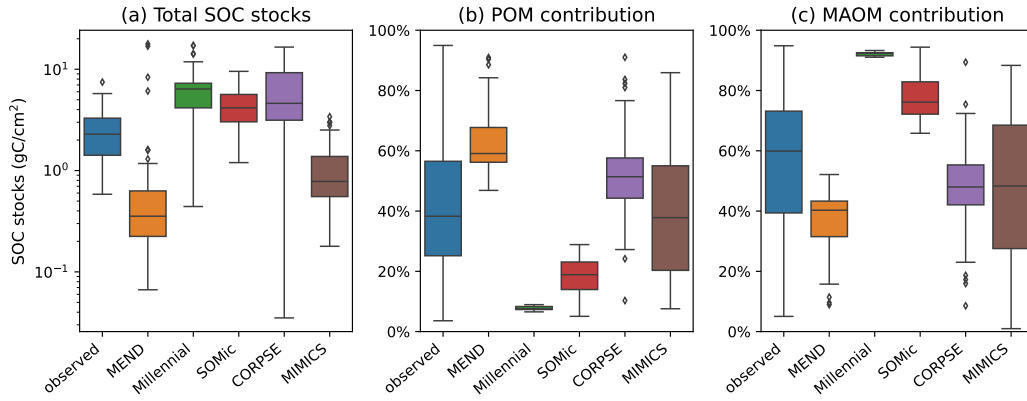


Figure 4. Observed and modeled total SOC stocks in the topsoil (top 5 or 10 cm of mineral soil) plotted on a log-transformed axis in subplot (a), and contributions of the POM and MAOM pools to the topsoil SOC stocks in subplots (b) and (c), respectively. Black diamonds are outliers. In (a), $n = 60$ for the boxplot of observed data, $n = 65$ for MEND, and $n = 77$ for all other models. In (b) and (c), $n = 77$ for all boxplots, except for MEND, where $n = 65$.

3.2 Performance with ^{14}C

With the notable exception of MIMICS, the new-generation models consistently overestimate the $\Delta^{14}\text{C}$ of bulk SOC, and their ^{14}C predictions do not capture the full variability of the observations (see Figure 5a). This is reminiscent of the ESMs' ^{14}C predictions (He et al., 2016), which also overestimate the $\Delta^{14}\text{C}$ of SOC and underestimate its variability. Therefore, our results could suggest that the new generation of soil models may be facing similar issues as the traditional SOC models incorporated into ESMs.

The pool-specific ^{14}C results, shown in Figure 5b-c, shed a more critical light on the performance of MIMICS with the $\Delta^{14}\text{C}$ of bulk SOC. MIMICS overestimates the $\Delta^{14}\text{C}$

of POM by 80‰ and underestimates the $\Delta^{14}\text{C}$ of MAOM by around 40‰ on average, and these biases happen to cancel out in such a way that MIMICS produces very good predictions for the $\Delta^{14}\text{C}$ of bulk SOC with a RMSE of just 80‰ and no bias, the best performance among the evaluated models (see Table 2). All five models overestimate the $\Delta^{14}\text{C}$ of POM, with an average positive bias of 67‰, and SOMic, Millennial, and MEND also overestimate MAOM $\Delta^{14}\text{C}$ by 74‰ on average. CORPSE is good at predicting the $\Delta^{14}\text{C}$ of MAOM with effectively no bias, but its POM $\Delta^{14}\text{C}$ predictions have the largest bias (+119‰) among all the models. On average, the evaluated models have a positive bias between 36‰ and 67‰, and a RMSE around 100‰ in their $\Delta^{14}\text{C}$ predictions for the POM, MAOM, and bulk SOC (see Table 2 for more details).

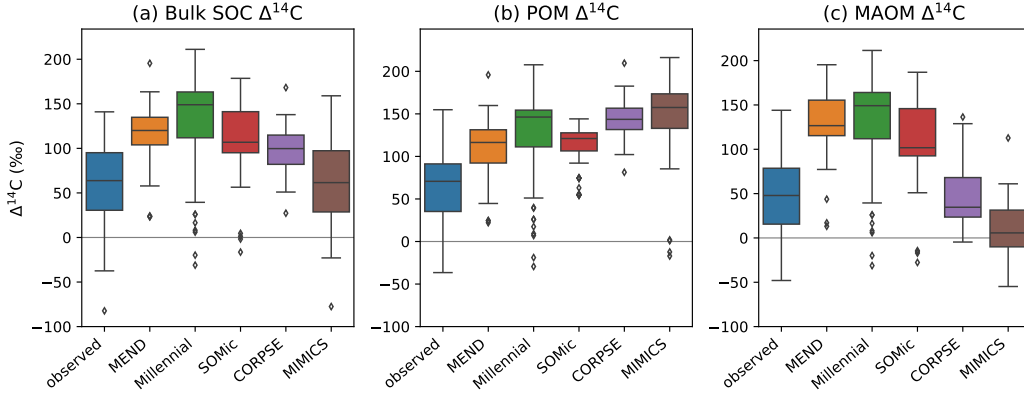


Figure 5. Observed and modeled $\Delta^{14}\text{C}$ of total SOC (a), POM (b), and MAOM (c) in the topsoil (top 5 or 10 cm of mineral soil). Black diamonds are outliers. Note that some extreme outliers are outside of plotting range. To have a uniform and consistent ^{14}C dataset, we excluded the 1949 and 1978 samples so that we end up with more compact data spanning only 18 years at the tail end of the bomb spike. Therefore, $n = 75$ for all boxplots, except for MEND's, where $n = 62$.

The models produce contrasting predictions for the evolution of soil ^{14}C over the second half of the 20th century. In the example of an alpine pasture (Figure 6), we can see that the CORPSE, SOMic and MIMICS models predict $\Delta^{14}\text{C}$ curves for POM which are distinct from MAOM, while the MEND and Millennial models produce similar $\Delta^{14}\text{C}$ dynamics for POM and MAOM. That is because the Millennial and MEND models have faster turnover rates than the other models, and their pools rapidly exchange carbon between themselves.

3.3 Role of environmental parameters

We further investigate how simulations depend on soil temperature and clay content, as these are considered some of the most important factors controlling SOC turnover and persistence (Basile-Doelsch et al., 2020; Leifeld et al., 2009).

Higher soil temperatures enhance microbial activity and generally increase the turnover rate of carbon in soils (German et al., 2012; Leifeld et al., 2009; Sierra et al., 2015). While the observed SOC stocks and POM and MAOM contributions are not correlated with temperature (Figure 7a-c), the observed $\Delta^{14}\text{C}$ of POM, MAOM, and bulk SOC significantly increase with higher temperature (Figure 7d-f), probably due to shorter carbon residence times in warmer soils. In contrast, the predicted $\Delta^{14}\text{C}$ of POM, MAOM, and bulk SOC are either uncorrelated or negatively correlated with soil temperature. All of

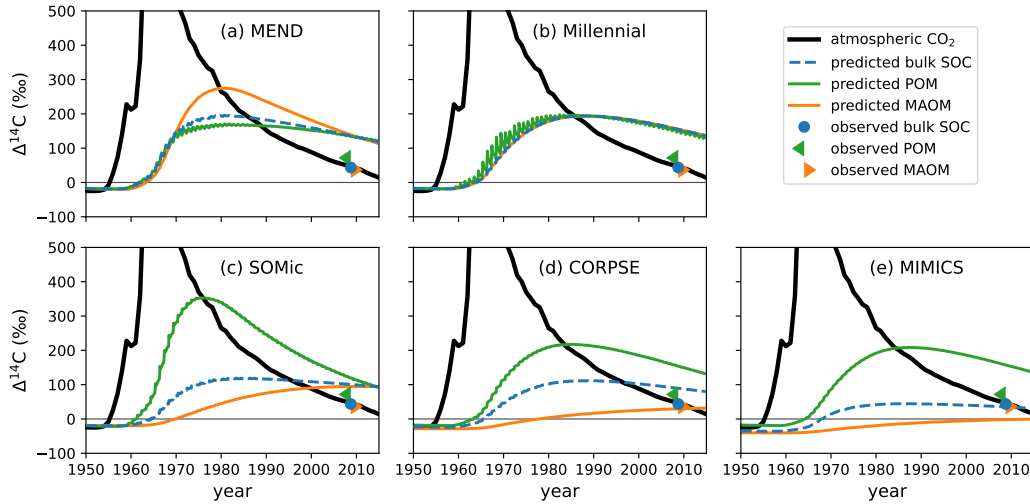


Figure 6. Observed and predicted $\Delta^{14}\text{C}$ of POM, MAOM, and bulk SOC in the top 10 cm of the mineral soil of a pasture in the Matsch valley, Italy. The observed ^{14}C data from 2008 are published in Meyer et al. (2012). The atmospheric $\Delta^{14}\text{CO}_2$ of the Northern Hemisphere (Graven et al., 2017) is shown for reference. With the SOMic, CORPSE and MIMICS models, the predicted $\Delta^{14}\text{C}$ of POM is distinct from the predicted $\Delta^{14}\text{C}$ of MAOM. On the other hand, the POM and MAOM pools in MEND and Millennial have very similar $\Delta^{14}\text{C}$ signals throughout the bomb-spike period.

the selected models modify carbon decomposition rates with a temperature-dependent scaling factor (Abramoff et al., 2022; Woolf & Lehmann, 2019; Kyker-Snowman et al., 2020; G. Wang et al., 2022; Sulman et al., 2014), but these results could indicate that they may need to increase or change the effect of temperature on carbon turnover rates.

In Figure 8c, the clay content of the sampled topsoils seems to be a decisive factor controlling the observed contribution of MAOM carbon to the total SOC stocks, with higher clay content correlating with higher MAOM contribution. This is also true for the MAOM contributions predicted by the MIMICS and CORPSE models, which produce the most accurate predictions of MAOM contribution (see Table 2). However, MIMICS appears to struggle with correctly simulating the effects of increased clay content on overall SOC dynamics, as evidenced by the inaccurate relationships of SOC stocks and $\Delta^{14}\text{C}$ with clay (see Figure 8a and Figure 8d-f). It appears that MIMICS correctly reproduces the evolution of MAOM contribution with clay content by increasing the residence time of carbon in MAOM, which in turn lowers the $\Delta^{14}\text{C}$ of MAOM and increases SOC stocks, contrary to the observations.

4 Discussion

The comparison of new-generation model predictions with ^{14}C observations reveals inaccuracies in the estimations of the time scales of carbon exchanges and stabilization in soils. Just like ESMs, most new-generation models overestimate the $\Delta^{14}\text{C}$ of bulk soil organic carbon (SOC) and they, too, may therefore be overestimating the effectiveness of soils as a net atmospheric CO_2 sink in the 21st century (He et al., 2016). The biases in the predictions of the repartition of SOC between particulate organic matter (POM) and mineral-associated organic matter (MAOM) may also affect the accuracy of future projections. POM and MAOM have been shown to have different sensitivities to envi-

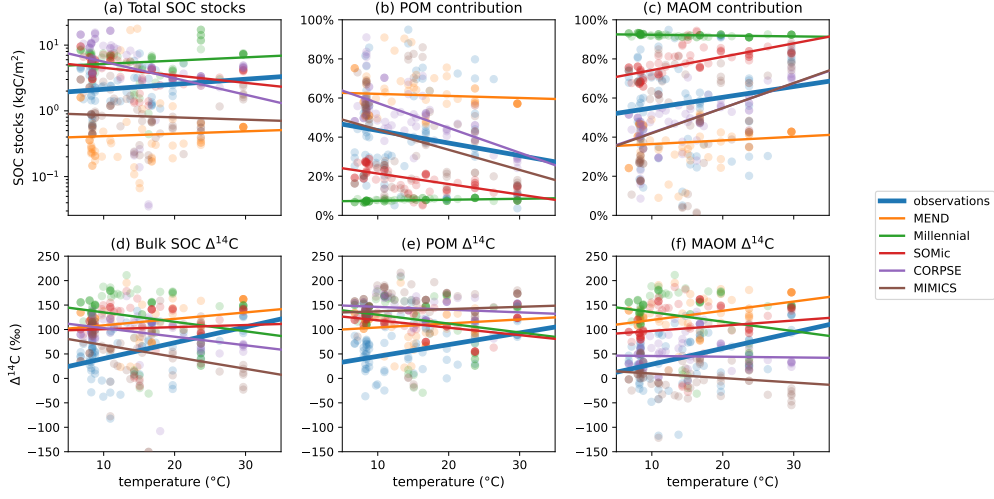


Figure 7. Relationship of observed and predicted carbon and $\Delta^{14}\text{C}$ data with respect to mean annual temperature of the topsoil (averaged over the 1970-2010 period). Circles are data-points, and lines are best linear fits through the points. The observed $\Delta^{14}\text{C}$ of bulk SOC, POM, and MAOM have a strong positive relationship with temperature. Meanwhile, the predicted $\Delta^{14}\text{C}$ are more weakly and sometimes negatively correlated with temperature. The linear fit line of CORPSE in subplot (c) is completely covered by the linear fit line of MIMICS. Note that we once again excluded the 1949 and 1978 samples for these plots.

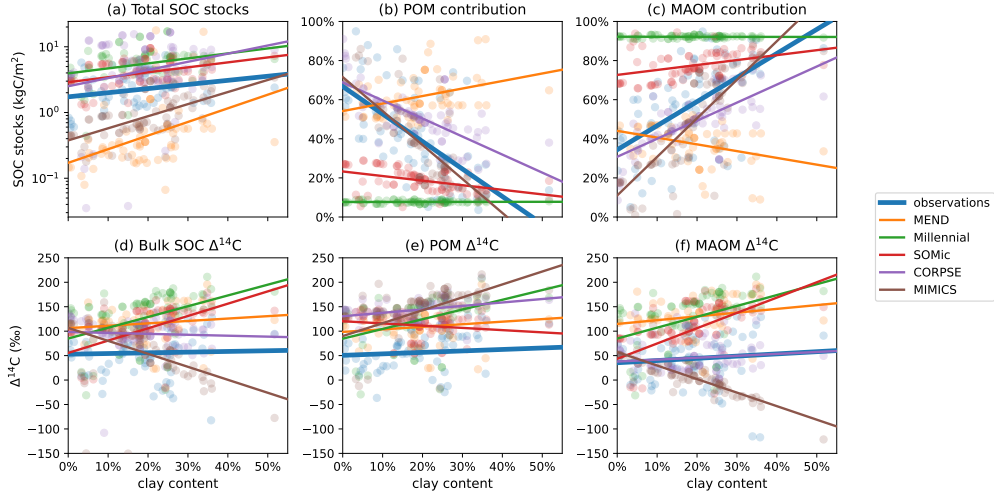


Figure 8. Relationship of observed and predicted carbon and $\Delta^{14}\text{C}$ data with respect to clay content in the topsoil. Circles are datapoints, and lines are best linear fits through the points. CORPSE and MIMICS successfully reproduce the positive relationship between topsoil clay content and the observed MAOM contribution to total SOC stocks in subplot (c). However, in subplot (f), MIMICS has a strong negative correlation of MAOM $\Delta^{14}\text{C}$ with clay content, unlike the observations, which do not show a correlation. The linear fit line of CORPSE in subplot (f) overlaps with that of the observations. Note that we once again excluded the 1949 and 1978 samples for these plots.

ronmental variables such as temperature and are thus expected to react differently to a changing climate (Hicks Pries et al., 2017; Kleber et al., 2011). Therefore, if models do not correctly partition SOC into POM and MAOM and misrepresent their ^{14}C , they will probably produce inaccurate predictions of SOC dynamics under climate change.

We identify three likely reasons why the new-generation models generally underperform with ^{14}C , and discuss how these problems could potentially be solved:

1. Insufficient datasets for the calibration of carbon turnover rates,
2. Lack of a “passive” pool with very slow turnover to account for inert SOC components,
3. Modeled pools do not capture the full range of SOC turnover rates.

The last point raises questions on the effectiveness of the new-generation models and the POM-MAOM distinction as a whole. This invites further research on the stability of the different constituents of SOC and a discussion on the most effective way to partition SOC into representative measurable pools.

4.1 Insufficient calibration datasets

Our ^{14}C results suggest that the new-generation models selected for this study overestimate some carbon turnover rates. The most extreme case is Millennial v2, which gives its micro-aggregate pool and mineral-adsorbed carbon pool turnover times of just a few months (see section S5 of supplement). On the other hand, ^{14}C -based studies find that the MAOM fraction, which includes micro-aggregates and mineral-adsorbed carbon, typically turns over on time scales of many decades or centuries (Gaudinski et al., 2000; Schrumpp & Kaiser, 2015; van der Voort et al., 2017; Baisden et al., 2002). The overestimation of turnover rates may be due to inadequate or insufficient data for the calibration of the models’ turnover parameters. Even though new-generation models have measurable pools, they do not usually assimilate pool-specific carbon and ^{14}C data, probably because such data are currently very sparse. The only models in our evaluation to calibrate their parameters with pool-specific carbon data are CORPSE (with data from only 2 soil profiles, according to Y. Zhang et al., 2021, Table S1) and Millennial (as described in Abramoff et al., 2022), and none of them assimilated pool-specific ^{14}C data. Instead, new-generation models primarily rely on less informative bulk soil data, as well as some soil incubation results, for parameter optimization. However, as the dataset of fraction-specific carbon and ^{14}C measurements is growing larger, new-generation models should start to take full advantage of the measurability of their pools and assimilate those highly informative data.

4.2 Lack of passive pool

Another explanation for the consistent overestimation of soil $\Delta^{14}\text{C}$ by new-generation models is the inability of the models to account for the presence of practically inert compounds in the soil, which negatively offset the bulk $\Delta^{14}\text{C}$. For example, some soils with a history of wildfires may contain a considerable fraction of pyrogenic carbon, which is composed of highly durable aromatic compounds and can remain in soils over thousands of years (Eckmeier et al., 2009; Hajdas et al., 2007; Leifeld, 2008). Due to its extreme longevity, pyrogenic carbon is depleted in ^{14}C as a result of radioactive decay, bringing down the overall $\Delta^{14}\text{C}$ of both POM (van der Voort et al., 2017) and MAOM (Soucémariadin et al., 2019). In deeper soils, the $\Delta^{14}\text{C}$ of SOC can be even further depleted due to a larger proportion of petrogenic carbon, which is devoid of ^{14}C (van der Voort et al., 2019). Whereas the two major traditional SOC models explicitly account for such extremely old components with a “passive” pool (1000 year turnover time) in the Century model (Parton et al., 1987) and an “inert organic matter” pool (no turnover at all) in the RothC model (Coleman & Jenkinson, 1996), the new-generation models effectively force virtually in-

ert components to fit into their actively cycling carbon pools. By creating a passive pool to account for inert compounds such as pyrogenic carbon, the new-generation models would be able to lower the overall $\Delta^{14}\text{C}$ of POM and MAOM, and more accurately reproduce the measured ^{14}C data.

4.3 Search for more representative measurable pools

Finally, the underperformance of the models with respect to ^{14}C may also be due to a choice of pools which are not truly representative of the full spectrum of turnover rates of the different SOC components. Whereas traditional models simply define the number and turnover rates of their SOC pools such that they can reproduce observed SOC dynamics while minimizing degrees of freedom, new-generation models also need to make sure their pools are at once easily measurable and representative of the various time scales of soil carbon persistence. If a measurable pool contains two or more components with very different turnover rates, the model may not be able to correctly reproduce the $\Delta^{14}\text{C}$ of that pool because it assumes a single, homogeneous turnover rate for the entire carbon pool. Although some models already split POM into various subpools with contrasting turnover times (e.g., soluble and insoluble litter pools in SOMic, or oxidizable and hydrolysable POM pools in MEND), they miss the most recalcitrant POM pool of pyrogenic carbon, which even in minute amounts can significantly alter the $\Delta^{14}\text{C}$ and apparent turnover of POM (Leifeld, 2008). Some new-generation models subdivide the MAOM pool into micro-aggregates and mineral-adsorbed carbon (e.g., Millennial), or into an active layer of adsorbed DOC and a more stable MAOM component (e.g., MEND). However, those MAOM subpools might still not be homogeneous enough in their turnover times for effective ^{14}C simulations. Recent ^{14}C studies determining the stability of MAOM under the action of peroxide oxidation show that it may be necessary to further split clay-sized MAOM into two measurable subpools which are decomposable or resistant to microbial exo-enzymes (Schrumpf et al., 2021; Jagadamma et al., 2010). Additionally, “continuous” SOC fractionation methods such as ramped pyrolysis oxidation (Stoner et al., 2023) could provide a much higher resolution of the SOC turnover rate spectrum. However, the resulting measurable pools are more difficult to interpret in terms of their role in the soil carbon cycle, and their incorporation into mechanistic SOC models is therefore less straightforward.

4.4 Limitations of this study

The accuracy of our model evaluation is affected by multiple factors. Though we took care to accurately match the modeled pools to the measured fractions (see section S2 in Supporting Information), the correspondences are imperfect and further complicated by non-standardized definitions and density cut-offs for the light and heavy fractions published on ISRaD. Nevertheless, this does not change the overall overestimation of soil $\Delta^{14}\text{C}$ by most models. The use of forcing data from possibly inaccurate CESM2-LE and CCMI outputs with low spatial resolution may also affect the accuracy of our model evaluation. Furthermore, the $\Delta^{14}\text{C}$ of the carbon inputs from the CESM2-LE product could be inaccurate, especially in soils with a thick organic layer, which pre-ages the carbon before it enters the mineral soil. However, the consistency and magnitude of the models’ overestimation of the topsoil’s $\Delta^{14}\text{C}$ with respect to observed data indicate that this overestimation is evidently a real pattern among the studied models. Finally, it is also important to note that our study only produces an incomplete picture of model performances on a global scale, since most of the measured datapoints represent North American and European forest ecosystems.

5 Summary

Despite their incorporation of the latest advances in soil sciences, new-generation soil organic carbon (SOC) models currently show similar discrepancies with ^{14}C data as the traditional SOC models. The new-generation models' consistent overestimation of the $\Delta^{14}\text{C}$ in both particulate organic matter (POM) and mineral-associated organic matter (MAOM) and their inaccurate partitioning of SOC between POM and MAOM suggest that these models underestimate the time scales of carbon storage in soils and might produce unreliable future predictions under climate change. To improve their predictions, new-generation models should take advantage of the measurability of their pools and calibrate their parameters with the rapidly growing dataset of pool-specific carbon and ^{14}C measurements in addition to incubation and bulk soil data. They may also have to reconsider their model design and simulate measurable pools which better capture the full spectrum of carbon turnover rates present in the soils. In particular, the consideration of highly persistent soil carbon such as pyrogenic carbon could significantly improve ^{14}C predictions. As more effective measurable pools are being discovered and the dataset of pool-specific ^{14}C data is expanding, new-generation soil models have the potential to eventually supersede the traditional SOC models employed by ESMs if they take full advantage of the measurability of their pools and assimilate the available data.

6 Open Research

The source code to download the input data, run the models, and reproduce all the results presented in this manuscript is available on our GitHub repository <https://github.com/asb219/evaluate-SOC-models>.

Our final implementations of Millennial, CORPSE, MIMICS, and the ^{14}C component of MEND are available as python modules in our repository. For the carbon and nitrogen components of MEND, the Fortran source code is in <https://github.com/asb219/MEND> (forked from <https://github.com/wanggangsheng/MEND>), which is added as a "git submodule" to our repository. We use the `install_github` function of the `devtools` package in R to compile the C++ code of the SOMic model released as "v1.1-asb219" in <https://github.com/asb219/somic1> (forked from <https://github.com/domwoolf/somic1>) and install it as an R package. We download data from SoilGrids with the `soilgrids` python package (<https://github.com/gantian127/soilgrids>).

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References

- Abramoff, R. Z., Guenet, B., Zhang, H., Georgiou, K., Xu, X., Viscarra Rossel, R. A., ... Ciais, P. (2022, January). Improved global-scale predictions of soil carbon stocks with Millennial Version 2. *Soil Biology and Biochemistry*, 164, 108466. Retrieved 2022-01-19, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071721003400> doi: 10.1016/j.soilbio.2021.108466
- Abramoff, R. Z., Xu, X., Hartman, M., O'Brien, S., Feng, W., Davidson, E., ... Mayes, M. A. (2018, January). The Millennial model: in search of measurable pools and transformations for modeling soil carbon in the new century. *Biogeochemistry*, 137(1-2), 51–71. Retrieved 2021-03-21, from <http://link.springer.com/10.1007/s10533-017-0409-7> doi: 10.1007/s10533-017-0409-7
- Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schrumpf, M., & Reichstein, M.

- (2015, September). Contribution of sorption, DOC transport and microbial interactions to the ^{14}C age of a soil organic carbon profile: Insights from a calibrated process model. *Soil Biology and Biochemistry*, 88, 390–402. Retrieved 2022-05-29, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071715002138> doi: 10.1016/j.soilbio.2015.06.008
- Ahrens, B., Guggenberger, G., Rethemeyer, J., John, S., Marschner, B., Heinze, S., ... Schrumpf, M. (2020, September). Combination of energy limitation and sorption capacity explains ^{14}C depth gradients. *Soil Biology and Biochemistry*, 148, 107912. Retrieved 2022-07-10, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071720302091> doi: 10.1016/j.soilbio.2020.107912
- Armstrong, D. G., Cook, H., & Thomas, B. (1950, January). The lignin and cellulose contents of certain grassland species at different stages of growth. *The Journal of Agricultural Science*, 40(1-2), 93–99. Retrieved 2023-11-25, from https://www.cambridge.org/core/product/identifier/S002185960004555X/type/journal_article doi: 10.1017/S002185960004555X
- Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., ... Ziehn, T. (2020, August). Carbon-concentration and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences*, 17(16), 4173–4222. Retrieved 2023-03-09, from <https://bg.copernicus.org/articles/17/4173/2020/> doi: 10.5194/bg-17-4173-2020
- Baisden, W. T., Amundson, R., Cook, A. C., & Brenner, D. L. (2002, December). Turnover and storage of C and N in five density fractions from California annual grassland surface soils: TURNOVER AND STORAGE OF C AND N. *Global Biogeochemical Cycles*, 16(4), 64–164–16. Retrieved 2023-07-01, from <http://doi.wiley.com/10.1029/2001GB001822> doi: 10.1029/2001GB001822
- Basile-Doelsch, I., Balesdent, J., & Pellerin, S. (2020, October). Reviews and syntheses: The mechanisms underlying carbon storage in soil. *Biogeosciences*, 17(21), 5223–5242. Retrieved 2023-08-28, from <https://bg.copernicus.org/articles/17/5223/2020/> doi: 10.5194/bg-17-5223-2020
- Berhe, A. A., Harden, J. W., Torn, M. S., Kleber, M., Burton, S. D., & Harte, J. (2012, June). Persistence of soil organic matter in eroding versus depositional landform positions: EROSION AND SOIL ORGANIC MATTER DYNAMICS. *Journal of Geophysical Research: Biogeosciences*, 117(G2), n/a–n/a. Retrieved 2023-07-01, from <http://doi.wiley.com/10.1029/2011JG001790> doi: 10.1029/2011JG001790
- Braakhekke, M. C., Beer, C., Hoosbeek, M. R., Reichstein, M., Kruijt, B., Schrumpf, M., & Kabat, P. (2011, May). SOMPROF: A vertically explicit soil organic matter model. *Ecological Modelling*, 222(10), 1712–1730. Retrieved 2021-04-21, from <https://linkinghub.elsevier.com/retrieve/pii/S03044380011000962> doi: 10.1016/j.ecolmodel.2011.02.015
- Braakhekke, M. C., Beer, C., Schrumpf, M., Ekici, A., Ahrens, B., Hoosbeek, M. R., ... Reichstein, M. (2014, March). The use of radiocarbon to constrain current and future soil organic matter turnover and transport in a temperate forest. *Journal of Geophysical Research: Biogeosciences*, 119(3), 372–391. Retrieved 2021-04-21, from <http://doi.wiley.com/10.1002/2013JG002420> doi: 10.1002/2013JG002420
- Braakhekke, M. C., Wutzler, T., Beer, C., Kattge, J., Schrumpf, M., Ahrens, B., ... Reichstein, M. (2013, January). Modeling the vertical soil organic matter profile using Bayesian parameter estimation. *Biogeosciences*, 10(1), 399–420. Retrieved 2021-04-21, from <https://bg.copernicus.org/articles/10/399/2013/> doi: 10.5194/bg-10-399-2013

- Cerli, C., Celi, L., Kalbitz, K., Guggenberger, G., & Kaiser, K. (2012, January). Separation of light and heavy organic matter fractions in soil — Testing for proper density cut-off and dispersion level. *Geoderma*, 170, 403–416. Retrieved 2022-01-23, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706111002941> doi: 10.1016/j.geoderma.2011.10.009
- Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., ... Cox, P. M. (2011, September). The Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, 4(3), 701–722. Retrieved 2021-04-14, from <https://gmd.copernicus.org/articles/4/701/2011/> doi: 10.5194/gmd-4-701-2011
- Coleman, K., & Jenkinson, D. S. (1996). RothC-26.3 - A Model for the turnover of carbon in soil. In D. S. Powlson, P. Smith, & J. U. Smith (Eds.), *Evaluation of Soil Organic Matter Models* (pp. 237–246). Berlin, Heidelberg: Springer Berlin Heidelberg. Retrieved 2021-03-24, from http://link.springer.com/10.1007/978-3-642-61094-3_17 doi: 10.1007/978-3-642-61094-3_17
- Crowther, T. W., Van Den Hoogen, J., Wan, J., Mayes, M. A., Keiser, A. D., Mo, L., ... Maynard, D. S. (2019, August). The global soil community and its influence on biogeochemistry. *Science*, 365(6455), eaav0550. Retrieved 2023-09-20, from <https://www.science.org/doi/10.1126/science.aav0550> doi: 10.1126/science.aav0550
- Danabasoglu, G., Lamarque, J., Bacmeister, J., Bailey, D. A., DuVivier, A. K., Edwards, J., ... Strand, W. G. (2020, February). The Community Earth System Model Version 2 (CESM2). *Journal of Advances in Modeling Earth Systems*, 12(2). Retrieved 2021-04-22, from <https://onlinelibrary.wiley.com/doi/10.1029/2019MS001916> doi: 10.1029/2019MS001916
- Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., ... Boeckx, P. (2015, October). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, 8(10), 780–783. Retrieved 2021-04-21, from <http://www.nature.com/articles/ngeo2516> doi: 10.1038/ngeo2516
- Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012, June). Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*, 18(6), 1781–1796. Retrieved 2021-04-21, from <http://doi.wiley.com/10.1111/j.1365-2486.2012.02665.x> doi: 10.1111/j.1365-2486.2012.02665.x
- Eckmeier, E., Van der Borg, K., Tegtmeier, U., Schmidt, M. W. I., & Gerlach, R. (2009). Dating Charred Soil Organic Matter: Comparison of Radiocarbon Ages from Macrocharcoals and Chemically Separated Charcoal Carbon. *Radiocarbon*, 51(2), 437–443. Retrieved 2022-02-07, from https://www.cambridge.org/core/product/identifier/S0033822200055831/type/journal_article doi: 10.1017/S0033822200055831
- Fan, X., Gao, D., Zhao, C., Wang, C., Qu, Y., Zhang, J., & Bai, E. (2021, August). Improved model simulation of soil carbon cycling by representing the microbially derived organic carbon pool. *The ISME Journal*, 15(8), 2248–2263. Retrieved 2022-07-10, from <http://www.nature.com/articles/s41396-021-00914-0> doi: 10.1038/s41396-021-00914-0
- Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., & Knutti, R. (2014, January). Uncertainties in CMIP5 Climate Projections due to Carbon Cycle Feedbacks. *Journal of Climate*, 27(2), 511–526. Retrieved 2022-09-19, from <http://journals.ametsoc.org/doi/10.1175/JCLI-D-12-00579.1> doi: 10.1175/JCLI-D-12-00579.1
- Friedlingstein, P., O’Sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., ... Zheng, B. (2022, November). Global Carbon Budget 2022. *Earth System Science Data*, 14(11), 4811–4900. Retrieved 2023-07-18,

- from <https://essd.copernicus.org/articles/14/4811/2022/> doi: 10.5194/essd-14-4811-2022
- Gaudinski, J. B., Trumbore, S. E., Davidson, E. A., & Zheng, S. (2000). Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*, 51(1), 33–69. Retrieved 2022-05-04, from <http://link.springer.com/10.1023/A:1006301010014> doi: 10.1023/A:1006301010014
- German, D. P., Marcelo, K. R. B., Stone, M. M., & Allison, S. D. (2012, April). The Michaelis-Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study. *Global Change Biology*, 18(4), 1468–1479. Retrieved 2021-04-19, from <http://doi.wiley.com/10.1111/j.1365-2486.2011.02615.x> doi: 10.1111/j.1365-2486.2011.02615.x
- Golchin, A., Oades, J., Skjemstad, J., & Clarke, P. (1994). Study of free and occluded particulate organic matter in soils by solid state ^{13}C CP/MAS NMR spectroscopy and scanning electron microscopy. *Soil Research*, 32(2), 285. Retrieved 2023-07-01, from <http://www.publish.csiro.au/?paper=SR9940285> doi: 10.1071/SR9940285
- Graven, H., Allison, C. E., Etheridge, D. M., Hammer, S., Keeling, R. F., Levin, I., ... White, J. W. C. (2017, December). Compiled records of carbon isotopes in atmospheric CO_2 for historical simulations in CMIP6. *Geoscientific Model Development*, 10(12), 4405–4417. Retrieved 2021-03-10, from <https://gmd.copernicus.org/articles/10/4405/2017/> doi: 10.5194/gmd-10-4405-2017
- Graven, H., Keeling, R. F., & Rogelj, J. (2020, November). Changes to Carbon Isotopes in Atmospheric CO_2 Over the Industrial Era and Into the Future. *Global Biogeochemical Cycles*, 34(11). Retrieved 2023-08-02, from <https://onlinelibrary.wiley.com/doi/10.1029/2019GB006170> doi: 10.1029/2019GB006170
- Griepentrog, M., Bodé, S., Boeckx, P., Hagedorn, F., Heim, A., & Schmidt, M. W. I. (2014, January). Nitrogen deposition promotes the production of new fungal residues but retards the decomposition of old residues in forest soil fractions. *Global Change Biology*, 20(1), 327–340. Retrieved 2022-02-11, from <https://onlinelibrary.wiley.com/doi/10.1111/gcb.12374> doi: 10.1111/gcb.12374
- Griepentrog, M., Eglinton, T. I., Hagedorn, F., Schmidt, M. W. I., & Wiesenberger, G. L. B. (2015, January). Interactive effects of elevated CO_2 and nitrogen deposition on fatty acid molecular and isotope composition of above- and belowground tree biomass and forest soil fractions. *Global Change Biology*, 21(1), 473–486. Retrieved 2021-09-26, from <https://onlinelibrary.wiley.com/doi/10.1111/gcb.12666> doi: 10.1111/gcb.12666
- Hajdas, I., Schlumpf, N., Minikus-Stary, N., Hagedorn, F., Eckmeier, E., Schoch, W., ... Cherubini, P. (2007, June). Radiocarbon ages of soil charcoals from the southern Alps, Ticino, Switzerland. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms*, 259(1), 398–402. Retrieved 2023-08-28, from <https://linkinghub.elsevier.com/retrieve/pii/S0168583X07004028> doi: 10.1016/j.nimb.2007.02.075
- Harden, J. W., Fries, T. L., & Pavich, M. J. (2002). Cycling of Beryllium and Carbon through hillslope soils in Iowa. *Biogeochemistry*, 60, 317–336. doi: 10.1023/A:1020308729553
- He, Y., Trumbore, S. E., Torn, M. S., Harden, J. W., Vaughn, L. J. S., Allison, S. D., & Randerson, J. T. (2016, September). Radiocarbon constraints imply reduced carbon uptake by soils during the 21st century. *Science*, 353(6306), 1419–1424. Retrieved 2022-05-28, from <https://www.sciencemag.org/lookup/doi/10.1126/science.aad4273> doi: 10.1126/science.aad4273

- Heckman, K. (2010). *Pedogenesis & Carbon Dynamics Across A Lithosequence Under Ponderosa Pine* (Doctoral dissertation). Retrieved 2023-10-06, from <https://zenodo.org/record/1486081> (Publisher: Zenodo)
- Heckman, K., Lawrence, C. R., & Harden, J. W. (2018, February). A sequential selective dissolution method to quantify storage and stability of organic carbon associated with Al and Fe hydroxide phases. *Geoderma*, 312, 24–35. Retrieved 2023-07-01, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706117312703> doi: 10.1016/j.geoderma.2017.09.043
- Hicks Pries, C. E., Castanha, C., Porras, R. C., & Torn, M. S. (2017, March). The whole-soil carbon flux in response to warming. *Science*, 355(6332), 1420–1423. Retrieved 2022-07-10, from <https://www.science.org/doi/10.1126/science.aal1319> doi: 10.1126/science.aal1319
- Hicks Pries, C. E., Sulman, B. N., West, C., O'Neill, C., Poppleton, E., Porras, R. C., ... Torn, M. S. (2018, October). Root litter decomposition slows with soil depth. *Soil Biology and Biochemistry*, 125, 103–114. Retrieved 2022-07-26, from <https://linkinghub.elsevier.com/retrieve/pii/S003807171830230X> doi: 10.1016/j.soilbio.2018.07.002
- Jagadamma, S., Lal, R., Ussiri, D. A. N., Trumbore, S. E., & Mestelan, S. (2010, April). Evaluation of structural chemistry and isotopic signatures of refractory soil organic carbon fraction isolated by wet oxidation methods. *Biogeochemistry*, 98(1-3), 29–44. Retrieved 2023-08-28, from <http://link.springer.com/10.1007/s10533-009-9374-0> doi: 10.1007/s10533-009-9374-0
- Kleber, M., Nico, P. S., Plante, A., Filley, T., Kramer, M., Swanston, C., & Sollins, P. (2011, February). Old and stable soil organic matter is not necessarily chemically recalcitrant: implications for modeling concepts and temperature sensitivity: SLOW TURNOVER OF LABILE SOIL ORGANIC MATTER. *Global Change Biology*, 17(2), 1097–1107. Retrieved 2022-01-28, from <https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2010.02278.x> doi: 10.1111/j.1365-2486.2010.02278.x
- Kyker-Snowman, E., Wieder, W. R., Frey, S. D., & Grandy, A. S. (2020, September). Stoichiometrically coupled carbon and nitrogen cycling in the Microbial-MIneral Carbon Stabilization model version 1.0 (MIMICS-CN v1.0). *Geoscientific Model Development*, 13(9), 4413–4434. Retrieved 2023-06-29, from <https://gmd.copernicus.org/articles/13/4413/2020/> doi: 10.5194/gmd-13-4413-2020
- Lavallee, J. M., Soong, J. L., & Cotrufo, M. F. (2020, January). Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology*, 26(1), 261–273. Retrieved 2021-12-08, from <https://onlinelibrary.wiley.com/doi/10.1111/gcb.14859> doi: 10.1111/gcb.14859
- Lawrence, C. R., Beem-Miller, J., Hoyt, A. M., Monroe, G., Sierra, C. A., Stoner, S., ... Wagai, R. (2020, January). An open-source database for the synthesis of soil radiocarbon data: International Soil Radiocarbon Database (ISRad) version 1.0. *Earth System Science Data*, 12(1), 61–76. Retrieved 2022-07-10, from <https://essd.copernicus.org/articles/12/61/2020/> doi: 10.5194/essd-12-61-2020
- Lehmann, J., & Kleber, M. (2015, December). The contentious nature of soil organic matter. *Nature*, 528(7580), 60–68. Retrieved 2021-04-21, from <http://www.nature.com/articles/nature16069> doi: 10.1038/nature16069
- Leifeld, J. (2008, May). Biased ¹⁴C-derived organic carbon turnover estimates following black carbon input to soil: an exploration with RothC. *Biogeochemistry*, 88(3), 205–211. Retrieved 2023-08-28, from <http://link.springer.com/10.1007/s10533-008-9209-4> doi: 10.1007/s10533-008-9209-4
- Leifeld, J., Zimmermann, M., & Fuhrer, J. (2008, December). Simulating decomposition of labile soil organic carbon: Effects of pH. *Soil Biol-*

- ogy and Biochemistry, 40(12), 2948–2951. Retrieved 2023-08-28, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071708002861>
doi: 10.1016/j.soilbio.2008.08.019
- Leifeld, J., Zimmermann, M., Fuhrer, J., & Conen, F. (2009, March). Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. *Global Change Biology*, 15(3), 668–679. Retrieved 2023-04-07, from <https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2008.01782.x> doi: 10.1111/j.1365-2486.2008.01782.x
- Liu, K., Xu, Y., Feng, W., Zhang, X., Yao, S., & Zhang, B. (2020, December). Modeling the dynamics of protected and primed organic carbon in soil and aggregates under constant soil moisture following litter incorporation. *Soil Biology and Biochemistry*, 151, 108039. Retrieved 2022-07-10, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071720303357>
doi: 10.1016/j.soilbio.2020.108039
- Lybrand, R. A., Heckman, K., & Rasmussen, C. (2017, August). Soil organic carbon partitioning and ^{14}C variation in desert and conifer ecosystems of southern Arizona. *Biogeochemistry*, 134(3), 261–277. Retrieved 2023-07-01, from <http://link.springer.com/10.1007/s10533-017-0360-7> doi: 10.1007/s10533-017-0360-7
- Malamoud, K., McBratney, A. B., Minasny, B., & Field, D. J. (2009, February). Modelling how carbon affects soil structure. *Geoderma*, 149(1-2), 19–26. Retrieved 2022-07-10, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706108003169> doi: 10.1016/j.geoderma.2008.10.018
- Marín-Spiotta, E., Swanston, C. W., Torn, M. S., Silver, W. L., & Burton, S. D. (2008, January). Chemical and mineral control of soil carbon turnover in abandoned tropical pastures. *Geoderma*, 143(1-2), 49–62. Retrieved 2023-07-01, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706107002807> doi: 10.1016/j.geoderma.2007.10.001
- McFarlane, K. J., Torn, M. S., Hanson, P. J., Porras, R. C., Swanston, C. W., Callahan, M. A., & Guilderson, T. P. (2013, March). Comparison of soil organic matter dynamics at five temperate deciduous forests with physical fractionation and radiocarbon measurements. *Biogeochemistry*, 112(1-3), 457–476. Retrieved 2023-07-01, from <http://link.springer.com/10.1007/s10533-012-9740-1> doi: 10.1007/s10533-012-9740-1
- Meyer, S., Leifeld, J., Bahn, M., & Fuhrer, J. (2012, February). Free and protected soil organic carbon dynamics respond differently to abandonment of mountain grassland. *Biogeosciences*, 9(2), 853–865. Retrieved 2023-10-06, from <https://bg.copernicus.org/articles/9/853/2012/> doi: 10.5194/bg-9-853-2012
- Mikutta, R., Turner, S., Schippers, A., Gentsch, N., Meyer-Stüve, S., Condon, L. M., ... Guggenberger, G. (2019, July). Microbial and abiotic controls on mineral-associated organic matter in soil profiles along an ecosystem gradient. *Scientific Reports*, 9(1), 10294. Retrieved 2023-08-28, from <https://www.nature.com/articles/s41598-019-46501-4> doi: 10.1038/s41598-019-46501-4
- Moore, J. A. M., Sulman, B. N., Mayes, M. A., Patterson, C. M., & Classen, A. T. (2020, April). Plant roots stimulate the decomposition of complex, but not simple, soil carbon. *Functional Ecology*, 34(4), 899–910. Retrieved 2022-08-29, from <https://onlinelibrary.wiley.com/doi/10.1111/1365-2435.13510> doi: 10.1111/1365-2435.13510
- Parton, W. J., Schimel, D. S., Cole, C. V., & Ojima, D. S. (1987, September). Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands. *Soil Science Society of America Journal*, 51(5), 1173–1179. Retrieved 2023-07-18, from <http://doi.wiley.com/10.2136/sssaj1987.03615995005100050015x> doi: 10.2136/sssaj1987.03615995005100050015x

- Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., ... Nieder, R. (2018, October). Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – A comprehensive method comparison. *Soil Biology and Biochemistry*, 125, 10–26. Retrieved 2022-07-10, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071718302232> doi: 10.1016/j.soilbio.2018.06.025
- Poggio, L., de Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., & Rossiter, D. (2021, June). SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *SOIL*, 7(1), 217–240. Retrieved 2022-09-25, from <https://soil.copernicus.org/articles/7/217/2021/> doi: 10.5194/soil-7-217-2021
- Rahman, M. M., Tsukamoto, J., Rahman, M. M., Yoneyama, A., & Mostafa, K. M. (2013, August). Lignin and its effects on litter decomposition in forest ecosystems. *Chemistry and Ecology*, 29(6), 540–553. Retrieved 2023-11-25, from <http://www.tandfonline.com/doi/abs/10.1080/02757540.2013.790380> doi: 10.1080/02757540.2013.790380
- Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., ... Wagai, R. (2018, February). Beyond clay: towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry*, 137(3), 297–306. Retrieved 2023-09-25, from <http://link.springer.com/10.1007/s10533-018-0424-3> doi: 10.1007/s10533-018-0424-3
- Rasmussen, C., Throckmorton, H., Liles, G., Heckman, K., Meding, S., & Horwath, W. (2018, July). Controls on Soil Organic Carbon Partitioning and Stabilization in the California Sierra Nevada. *Soil Systems*, 2(3), 41. Retrieved 2023-07-02, from <http://www.mdpi.com/2571-8789/2/3/41> doi: 10.3390/soilsystems2030041
- Roberts, M. L., & Southon, J. R. (2007). A Preliminary Determination of the Absolute $^{14}\text{C}/^{12}\text{C}$ Ratio of OX-I. *Radiocarbon*, 49(2), 441–445. Retrieved 2021-04-11, from https://www.cambridge.org/core/product/identifier/S0033822200042363/type/journal_article doi: 10.1017/S0033822200042363
- Robertson, A. D., Paustian, K., Ogle, S., Wallenstein, M. D., Lugato, E., & Cotrufo, M. F. (2019, March). Unifying soil organic matter formation and persistence frameworks: the MEMS model. *Biogeosciences*, 16(6), 1225–1248. Retrieved 2022-01-28, from <https://bg.copernicus.org/articles/16/1225/2019/> doi: 10.5194/bg-16-1225-2019
- Rodgers, K. B., Lee, S.-S., Rosenbloom, N., Timmermann, A., Danabasoglu, G., Deser, C., ... Yeager, S. G. (2021, December). Ubiquity of human-induced changes in climate variability. *Earth System Dynamics*, 12(4), 1393–1411. Retrieved 2022-09-25, from <https://esd.copernicus.org/articles/12/1393/2021/> doi: 10.5194/esd-12-1393-2021
- Rowley, M. C., Grand, S., & Verrecchia, E. P. (2018, January). Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry*, 137(1-2), 27–49. Retrieved 2023-09-25, from <http://link.springer.com/10.1007/s10533-017-0410-1> doi: 10.1007/s10533-017-0410-1
- Salazar, A., Sulman, B. N., & Dukes, J. S. (2018, January). Microbial dormancy promotes microbial biomass and respiration across pulses of drying-wetting stress. *Soil Biology and Biochemistry*, 116, 237–244. Retrieved 2023-06-25, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071717306120> doi: 10.1016/j.soilbio.2017.10.017
- Schimel, J. (2023, March). Modeling ecosystem-scale carbon dynamics in soil: The microbial dimension. *Soil Biology and Biochemistry*, 178, 108948. Retrieved 2023-11-18, from <https://linkinghub.elsevier.com/retrieve/pii/S003807172300010X> doi: 10.1016/j.soilbio.2023.108948
- Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G.,

- Janssens, I. A., ... Trumbore, S. E. (2011, October). Persistence of soil organic matter as an ecosystem property. *Nature*, 478(7367), 49–56. Retrieved 2022-02-11, from <http://www.nature.com/articles/nature10386> doi: 10.1038/nature10386
- Schrumpf, M., & Kaiser, K. (2015, February). Large differences in estimates of soil organic carbon turnover in density fractions by using single and repeated radiocarbon inventories. *Geoderma*, 239–240, 168–178. Retrieved 2022-02-06, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706114003577> doi: 10.1016/j.geoderma.2014.09.025
- Schrumpf, M., Kaiser, K., Guggenberger, G., Persson, T., Kögel-Knabner, I., & Schulze, E.-D. (2013, March). Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. *Biogeosciences*, 10(3), 1675–1691. Retrieved 2023-07-02, from <https://bg.copernicus.org/articles/10/1675/2013/> doi: 10.5194/bg-10-1675-2013
- Schrumpf, M., Kaiser, K., Mayer, A., Hempel, G., & Trumbore, S. (2021, February). Age distribution, extractability, and stability of mineral-bound organic carbon in central European soils. *Biogeosciences*, 18(3), 1241–1257. Retrieved 2023-08-28, from <https://bg.copernicus.org/articles/18/1241/2021/> doi: 10.5194/bg-18-1241-2021
- Segoli, M., De Gryze, S., Dou, F., Lee, J., Post, W., Denef, K., & Six, J. (2013, August). AggModel: A soil organic matter model with measurable pools for use in incubation studies. *Ecological Modelling*, 263, 1–9. Retrieved 2021-04-21, from <https://linkinghub.elsevier.com/retrieve/pii/S03044380013002147> doi: 10.1016/j.ecolmodel.2013.04.010
- Sierra, C. A., Trumbore, S. E., Davidson, E. A., Vicca, S., & Janssens, I. (2015, March). Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture. *Journal of Advances in Modeling Earth Systems*, 7(1), 335–356. Retrieved 2021-04-19, from <http://doi.wiley.com/10.1002/2014MS000358> doi: 10.1002/2014MS000358
- Soucémariadin, L., Reisser, M., Cécillon, L., Barré, P., Nicolas, M., & Abiven, S. (2019, June). Pyrogenic carbon content and dynamics in top and sub-soil of French forests. *Soil Biology and Biochemistry*, 133, 12–15. Retrieved 2023-08-28, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071719300537> doi: 10.1016/j.soilbio.2019.02.013
- Stamati, F. E., Nikolaidis, N. P., Banwart, S., & Blum, W. E. (2013, December). A coupled carbon, aggregation, and structure turnover (CAST) model for topsoils. *Geoderma*, 211–212, 51–64. Retrieved 2022-05-29, from <https://linkinghub.elsevier.com/retrieve/pii/S0016706113002140> doi: 10.1016/j.geoderma.2013.06.014
- Stoner, S. W., Schrumpf, M., Hoyt, A., Sierra, C. A., Doetterl, S., Galy, V., & Trumbore, S. (2023, August). How well does ramped thermal oxidation quantify the age distribution of soil carbon? Assessing thermal stability of physically and chemically fractionated soil organic matter. *Biogeosciences*, 20(15), 3151–3163. Retrieved 2023-08-26, from <https://bg.copernicus.org/articles/20/3151/2023/> doi: 10.5194/bg-20-3151-2023
- Sulman, B. N., Brzostek, E. R., Medici, C., Shevliakova, E., Menge, D. N. L., & Phillips, R. P. (2017, August). Feedbacks between plant N demand and rhizosphere priming depend on type of mycorrhizal association. *Ecology Letters*, 20(8), 1043–1053. Retrieved 2022-07-26, from <https://onlinelibrary.wiley.com/doi/10.1111/ele.12802> doi: 10.1111/ele.12802
- Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E., & Pacala, S. W. (2014, December). Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO₂. *Nature Climate Change*, 4(12), 1099–1102. Re-

- trieved 2022-05-29, from <http://www.nature.com/articles/nclimate2436>
doi: 10.1038/nclimate2436
- Tian, H., Yang, J., Lu, C., Xu, R., Canadell, J. G., Jackson, R. B., ... Zhu, Q. (2018, June). The Global N₂O Model Intercomparison Project. *Bulletin of the American Meteorological Society*, 99(6), 1231–1251. Retrieved 2023-06-20, from <https://journals.ametsoc.org/view/journals/bams/99/6/bams-d-17-0212.1.xml> doi: 10.1175/BAMS-D-17-0212.1
- Tipping, E., & Rowe, E. C. (2019, March). Modelling the physical states, element stoichiometries and residence times of topsoil organic matter. *European Journal of Soil Science*, 70(2), 321–337. Retrieved 2022-07-10, from <https://onlinelibrary.wiley.com/doi/10.1111/ejss.12785> doi: 10.1111/ejss.12785
- Trumbore, S. E., Sierra, C. A., & Hicks Pries, C. E. (2016). Radiocarbon Nomenclature, Theory, Models, and Interpretation: Measuring Age, Determining Cycling Rates, and Tracing Source Pools. In E. A. Schuur, E. Druffel, & S. E. Trumbore (Eds.), *Radiocarbon and Climate Change* (pp. 45–82). Cham: Springer International Publishing. Retrieved 2021-04-05, from http://link.springer.com/10.1007/978-3-319-25643-6_3 doi: 10.1007/978-3-319-25643-6_3
- van der Voort, T. S., Mannu, U., Hagedorn, F., McIntyre, C., Walthert, L., Schleppi, P., ... Eglinton, T. I. (2019, August). Dynamics of deep soil carbon – insights from ¹⁴C time series across a climatic gradient. *Biogeosciences*, 16(16), 3233–3246. Retrieved 2021-03-21, from <https://bg.copernicus.org/articles/16/3233/2019/> doi: 10.5194/bg-16-3233-2019
- van der Voort, T. S., Zell, C. I., Hagedorn, F., Feng, X., McIntyre, C. P., Haghipour, N., ... Eglinton, T. I. (2017, December). Diverse Soil Carbon Dynamics Expressed at the Molecular Level: Molecular Level Soil Carbon Dynamics. *Geophysical Research Letters*, 44(23), 11,840–11,850. Retrieved 2021-03-21, from <http://doi.wiley.com/10.1002/2017GL076188> doi: 10.1002/2017GL076188
- Vogel, C., Mueller, C. W., Höschen, C., Buegger, F., Heister, K., Schulz, S., ... Kögel-Knabner, I. (2014, January). Submicron structures provide preferential spots for carbon and nitrogen sequestration in soils. *Nature Communications*, 5(1), 2947. Retrieved 2023-09-20, from <https://www.nature.com/articles/ncomms3947> doi: 10.1038/ncomms3947
- von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., & Marschner, B. (2007, September). SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. *Soil Biology and Biochemistry*, 39(9), 2183–2207. Retrieved 2022-01-26, from <https://linkinghub.elsevier.com/retrieve/pii/S0038071707001125> doi: 10.1016/j.soilbio.2007.03.007
- Wagai, R., Mayer, L. M., & Kitayama, K. (2009, February). Nature of the “occluded” low-density fraction in soil organic matter studies: A critical review. *Soil Science and Plant Nutrition*, 55(1), 13–25. Retrieved 2022-05-29, from <http://www.tandfonline.com/doi/abs/10.1111/j.1747-0765.2008.00356.x> doi: 10.1111/j.1747-0765.2008.00356.x
- Wang, G., Gao, Q., Yang, Y., Hobbie, S. E., Reich, P. B., & Zhou, J. (2022, March). Soil enzymes as indicators of soil function: A step toward greater realism in microbial ecological modeling. *Global Change Biology*, 28(5), 1935–1950. Retrieved 2023-06-23, from <https://onlinelibrary.wiley.com/doi/10.1111/gcb.16036> doi: 10.1111/gcb.16036
- Wang, G., Jagadamma, S., Mayes, M. A., Schadt, C. W., Megan Steinweg, J., Gu, L., & Post, W. M. (2015, January). Microbial dormancy improves development and experimental validation of ecosystem model. *The ISME Journal*, 9(1), 226–237. Retrieved 2021-04-21, from <http://www.nature.com/articles/>

- ismej2014120 doi: 10.1038/ismej.2014.120
- Wang, G., Post, W. M., & Mayes, M. A. (2013, January). Development of microbial-enzyme-mediated decomposition model parameters through steady-state and dynamic analyses. *Ecological Applications*, 23(1), 255–272. Retrieved 2021-04-21, from <http://doi.wiley.com/10.1890/12-0681.1> doi: 10.1890/12-0681.1
- Wang, Y., Zhang, H., Ciais, P., Goll, D., Huang, Y., Wood, J. D., ... Prescher, A. (2021, April). Microbial Activity and Root Carbon Inputs Are More Important than Soil Carbon Diffusion in Simulating Soil Carbon Profiles. *Journal of Geophysical Research: Biogeosciences*, 126(4). Retrieved 2022-07-10, from <https://onlinelibrary.wiley.com/doi/10.1029/2020JG006205> doi: 10.1029/2020JG006205
- Wieder, W. R., Grandy, A. S., Kallenbach, C. M., & Bonan, G. B. (2014, July). Integrating microbial physiology and physio-chemical principles in soils with the Microbial-MIneral Carbon Stabilization (MIMICS) model. *Biogeosciences*, 11(14), 3899–3917. Retrieved 2021-05-25, from <https://bg.copernicus.org/articles/11/3899/2014/> doi: 10.5194/bg-11-3899-2014
- Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G., & Bonan, G. B. (2015, June). Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geoscientific Model Development*, 8(6), 1789–1808. Retrieved 2023-06-29, from <https://gmd.copernicus.org/articles/8/1789/2015/> doi: 10.5194/gmd-8-1789-2015
- Woolf, D., & Lehmann, J. (2019, December). Microbial models with minimal mineral protection can explain long-term soil organic carbon persistence. *Scientific Reports*, 9(1), 6522. Retrieved 2021-10-01, from <http://www.nature.com/articles/s41598-019-43026-8> doi: 10.1038/s41598-019-43026-8
- Xiao, L., Wang, G., Chang, J., Chen, Y., Guo, X., Mao, X., ... Luo, Z. (2023, August). Global depth distribution of belowground net primary productivity and its drivers. *Global Ecology and Biogeography*, 32(8), 1435–1451. Retrieved 2023-07-16, from <https://onlinelibrary.wiley.com/doi/10.1111/geb.13705> doi: 10.1111/geb.13705
- Yu, L., Ahrens, B., Wutzler, T., Schrumpf, M., & Zaehle, S. (2020, February). Jena Soil Model (JSM v1.0; revision 1934): a microbial soil organic carbon model integrated with nitrogen and phosphorus processes. *Geoscientific Model Development*, 13(2), 783–803. Retrieved 2022-07-10, from <https://gmd.copernicus.org/articles/13/783/2020/> doi: 10.5194/gmd-13-783-2020
- Zhang, H., Goll, D. S., Wang, Y., Ciais, P., Wieder, W. R., Abramoff, R., ... Tang, X. (2020, April). Microbial dynamics and soil physicochemical properties explain large-scale variations in soil organic carbon. *Global Change Biology*, 26(4), 2668–2685. Retrieved 2022-07-10, from <https://onlinelibrary.wiley.com/doi/10.1111/gcb.14994> doi: 10.1111/gcb.14994
- Zhang, Y., Lavallee, J. M., Robertson, A. D., Even, R., Ogle, S. M., Paustian, K., & Cotrufo, M. F. (2021, May). Simulating measurable ecosystem carbon and nitrogen dynamics with the mechanistically defined MEMS 2.0 model. *Biogeosciences*, 18(10), 3147–3171. Retrieved 2022-07-10, from <https://bg.copernicus.org/articles/18/3147/2021/> doi: 10.5194/bg-18-3147-2021